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JUL 5 - 1932

ECOLOGICAL MONOGRAPHS

VOL. II JULY, 1932 NO. 3

OFFICIAL PUBLICATION OF THE
ECOLOGICAL SOCIETY OF AMERICA

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PUBLISHED QUARTERLY BY
THE DUKE UNIVERSITY PRESS
DURHAM, N. C., U.S.A.

ECOLOGICAL MONOGRAPHS

A QUARTERLY JOURNAL
FOR ALL PHASES OF BIOLOGY

Issued on the fifteenth of December, March, June, and September

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Subscription price, $6.00 per year. Parts of volumes can be supplied at the rates for single numbers, $1.50 each. Missing numbers will be supplied free when lost in the mails if written notice is received by the Business Manager within one month of date of issue. All remittances should be made payable to the Duke University Press.

Agents in Great Britain: The Cambridge University Press, Fetter Lane, London, E. C. 4. Prices can be had on application.

Entered as Second-class Matter at the Postoffice at Durham, North Carolina.

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AQUATIC MOLLUSCA OF THE TIPPECANOE RIVER SYSTEM. PART I. POST-GLACIAL MIGRATION AND PRESENT DISTRIBUTION OF FOUR SPECIES OF SNAILS*

By

HERMAN P. WRIGHT

* Presented in partial fulfillment of the requirements for the degree Doctor of Philosophy, with a major in Zoölogy, at Indiana University, May, 1930.

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AQUATIC MOLLUSCA OF THE TIPPECANOE RIVER SYSTEM. PART I. POST-GLACIAL MIGRATION AND PRESENT DISTRIBUTION OF FOUR SPECIES OF SNAILS

INTRODUCTION

The study of the post-glacial distribution of fresh-water mollusca in North American has been approached in two ways: by an enumeration of species in the post-glacial deposits (vertical distribution), and by a study of the longitudinal distribution in streams. Vertical sections in the post-glacial deposits have been made in scattered localities, and the shells have been referred to various species. Baker (1920) brought most of this literature together in his volume *Life of the Pleistocene*. Since that date Sterki (1920) has recorded species from marl beds in Ohio. Adams (1915), Ortmann (1920, 1924), and Baker (1922, 1927) studied longitudinal distribution in streams, correlating it in each case with the physiographic development of the region.

In the present study both lines of approach have been used. Vertical distribution has been studied by making borings in the post-glacial deposits of the Tippecanoe River region, and longitudinal distribution by methodical collecting in the Tippecanoe River and its tributaries. By comparing the two, it has been possible to demonstrate the routes of migration into (and the total area of distribution within) the Tippecanoe River basin of four species of aquatic gastropods, *Goniobasis livescens* Menke, *Pleurocera acuta* Rafinesque, *Campeloma rufum* Haldeman, and *Viviparus contectoides* Binney.

The writer wishes to express his gratitude to the Zoölogy Faculty of Indiana University, especially to Dr. Will Scott for his kindly interest, his helpful suggestions, and his coöperation, without which he could not have secured the necessary material equipment; to the Graduate Council of Indiana University for the grant of two University fellowships during 1927-28 and 1929-30; to Dr. Fernandus Payne, Dean of the Graduate School, Indiana University, for making field work possible during the summers of 1927 and 1928 by means of grants from the Waterman Research Foundation; to Dr. Ira T. Wilson, Professor of Biology, Heidelberg College, Tiffin, Ohio, for first arousing the writer's interest in the study of fresh-water Mollusca, furnishing transportation, assisting with field work, and giving constructive criticism from time to time; to Dr. Frank C. Baker, Curator of the Museum of Natural History, University of Illinois, and to Mr. Calvin Goodrich, Museum of Zoölogy, University of Michigan, for identifying the four species of gastropods on which this study is based.

The author desires, also, to express his indebtedness to Mr. Raymond J. Myers, who accompanied him on numerous collecting trips; to his wife,

Christina S. Wright, who assisted in various ways; and to the many local inhabitants of the Tippecanoe region who permitted him to trespass on their property and frequently allowed him the use of their boats for collecting.

During the course of the study, 90 lakes of the river system were examined, and collections were made at various places on each lake. In addition, the connecting streams between lakes and the outlets of the lakes into the river were explored and collections taken. Two trips were made by row-boat, a ten day trip from Warsaw to Monticello, and a two weeks trip from Warsaw to the mouth of the Tippecanoe. On these trips, collections were taken at one to five mile intervals, and repeated observations were made between collections. The field work extended over four summers (1925-1928). More than 1,000 collections of living or fossil shells were taken, each representing a distinct locality, except in marl borings where different strata in the same boring were represented by separate collections.

The collections are usually large; frequently a single collection contains 1,500 to 2,000 specimens. About 70 species of aquatic Mollusca are represented in the writer's collections of the Tippecanoe Region. Four of the larger species have been selected on which to base this study. It is planned to make similar studies of the other 70 or more species of Tippecanoe River Mollusca. Upon completion of the Tippecanoe survey, the writer proposes to make intensive studies of the past and present distribution of Mollusca, especially of the *Sphaeriidae* and *Pleuroceridae*, in other river systems. Ultimately, he hopes to trace the fresh-water snail fauna through the various stages that led to its present widespread distribution throughout the glaciated portions of the United States and Canada. A study of this sort will be of interest in showing the facts of migration, and will give much needed information on taxonomic relationships of the various species: their evolution, their value as index animals, and the effect upon them of various types of environment. The writer believes that such correlation between past and present distribution will be a new and effective method of studying post-glacial molluscan migration—a method which, thus far, is yielding gratifying results.

METHODS

Intensive collecting under varying conditions demanded flexibility in collecting methods. In deep water, a naturalist's dredge was towed with a row boat. Where the water was shallow, wading was more convenient; in such places, a scoop dredge of the writer's own design was ordinarily used. Where the bottom was muddy, the material was usually washed through a box-sieve. On bowlder bottom, hand-picking was frequently practiced. Quantitative methods, to show relative abundance, were occasionally employed, but were always supplemented with qualitative collections from the same locality so as to add numbers to the material for study.

Marl samples were taken with a post-hole auger. The length of the handle could be extended by four-foot sections when necessary, so that the maximum sampling depth was 58 feet. Samples were taken at different levels according to the stratification of the deposit. Each sample was treated as a separate collection. The borings shown in Figs. 4 to 10 are not "selected." Frequently, several borings are shown for the same lake, only one of which contains fossils. In such cases, the other borings were taken in unlikely situations; for example, in swamps or embayments which were probably extinct before the arrival of snails in this locality. Through experience, it was learned that borings taken near the present shore-line of the lakes are most likely to demonstrate the existence of fossils.

In the field each collection was put into a muslin bag, together with a label bearing the field number, location, and date. The labels were inclosed in glass vials for protection. All collections, except those taken from marl, were placed in alcohol for at least a few days before being dried. A printed form card was used in recording data.

PHYSIOGRAPHY[1]

The physiography of this region has been discussed by Dryer (1891 and 1893), Leverett and Taylor (1915), Malott (1922), and Tucker (1922). The following is a brief summary of the present state of our knowledge based in part on the above references and in part on original field observations.

The Tippecanoe River is a northern tributary of the Wabash. Its length is 166 miles, and its basin contains approximately 1,890 square miles. It lies wholly within the region covered by the Wisconsin glaciation. Developmentally it is divided into two distinct parts. The upper part flows slightly south of west and the lower part flows generally south. This change in the course of the river occurs near the town of Ora. The upper part of the river runs along the northern edge of the interlobate moraine of the Saginaw and the Huron-Erie lobes. This moraine has been called the Packerton Moraine (Malott, 1922). The great majority of the 95 lakes drained by the Tippecanoe lie in depressions in this moraine.

Here during the Wisconsin glaciation the thinner Saginaw Lobe met and was overridden by the more massive Huron-Erie Lobe. With the wasting of the ice along the northern border of this mass came the genesis of the Tippecanoe River. At this period it discharged to the northwest to the Kankakee or to the west through what is now the Iroquois River. Just what incident turned these waters from the west and north toward the south to the Wabash is not certainly known. It has been suggested that the plain along the Kankakee had been built up by the sand carrying waters from the northeast until

[1] Dr. Wright died Nov. 1930. In preparing his manuscript for press, it was divided into two parts. The detailed description of the physiography of the Tippecanoe River is published in Proc. Ind. Acad. Sci.: 40. This section was condensed from the materials of Dr. Wright. However, the undersigned is wholly responsible for the view expressed in the third paragraph of this section.—WILL SCOTT.

it obstructed the Tippecanoe discharge. It may be that the lower Tippecanoe developed independently and by a mild piracy captured the westward flowing part of the river. The final solution of this problem must await a detailed and critical study of this area.

About half-way down this lower part of the river it crosses the hard limestones of the Cincinnati anticline. These erode very slowly. The result is that from this point (Norway) to the Wabash Valley, the Tippecanoe is very rapid. This river is rather anomalous in that in its upper course it meanders with a gentle even current over slightly dissected glacial deposits, while in its lower course it is a series of rapids over bedrock. The data indicate that the snails considered in this study were derived for the most part from the Kankakee to the north and west. A small invasion fom the St. Joseph of Michigan occurred as the result of a sort of artificial stream piracy.

For convenience in discussion, the river has been divided rather arbitrarily into an upper, middle, and lower course. The upper is defined as that part of the stream between the head waters in Crooked Lake and the point where the river crosses the Fulton-Marshall County line; the middle course extends from the Fulton-Marshall County line to the village of Norway; and the lower course is the region between Norway and the mouth of the river in northeastern Tippecanoe County.

DATA

Lower Course

Campeloma rufum is the only one of the four species present in the lower course of the river. It occurs in small numbers along the protected sand and gravel margins of the stream from the Oakdale Dam to the mouth of the river (Fig. 13). Nowhere is it found in great numbers.

Upstream from the Oakdale Dam no snails are found for about thirty miles; Campeloma appears again near the village of Pulaski, in southern Pulaski County. It has evidently migrated a few miles up the mouth of the Tippecanoe River to the Oakdale Dam from the Wabash.

Middle Course

The four species studied are all found in the middle course of the Tippecanoe River. *Viviparus contectoides,* however, is confined to Maxinkuckee Lake and its outlet (Fig. 14). The other three species are found throughout the middle course of the Tippecanoe River, except below Pulaski; ordinarily their distribution is in colonies rather than continuous. At Winamac, however, there is a more or less continuous colony several miles in extent.

Upstream, from the outlet of Bruce Lake to Ora, colonies are very scarce. The bottom here is shifting, composed mostly of sand. The sandy and bowlder strewn channel from Ora to Leiters Ford is very sparsely inhabited by the three species. The firm silty sand margins from Leiters Ford to the

highway bridge (U. S. 31), three miles north of Rochester, support the largest snail population of the middle course. The remainder of the middle course, with its increasing mid-stream vegetation, has a larger area which is suitable for Goniobasis and Pleurocera. Campeloma, even here, is largely confined to the borders of the stream. It is usually found burrowing in the sand or silty sand in less than one foot of water.

In the middle course, the Tippecanoe River receives several tributaries which are not outlets of lakes. Starting at Norway and going upstream, the principal ones are Honey, Swigman, Keane, Little Monon, Big Monon, Indian, and Big Mill. Big Mill Creek was thoroughly searched and some sporadic collecting was done in the other streams, but no specimens were found.[1]

Fletcher Lake. This lake does not support any of the species under consideration. The outlet of Fletcher Lake is an intermittent tributary of Indian Creek. The absence of all four species, both living and fossil, in Indian Creek explains their non-existence in Fletcher Lake.

Bruce Lake. A boring (Fig. 4) made in 2 feet of water, at the end of the sand-bar that projects from the eastern shore, opposite Showley's Park, shows the following stratification: shell-less marl, 3 feet; mixed sand and marl; 0.5 foot, containing fossil shells of Goniobasis; sand, 5 feet; shell-less marl, 3 feet; morainic sand. The stream leading from the outlet of Bruce Lake is about five miles in length. No living shells were taken from this, but a few badly eroded fossils of Campeloma were found in the dredging along its banks, about 2½ miles from the lake. The stream is marshy throughout, but increasingly so near the lake. About a mile from Bruce Lake (T31N, R1W, sec. 36) is a slough containing an accumulation of peat 54 feet deep, covering a shell-less marl deposit (Fig. 4).

Langhabaugh, Hart's, and Leopold Lakes. These three lakes lie on the crest of a low moraine (Fig. 3). Sections made in embayments along their margins revealed strata of peat covering sand (Fig. 4). At other places, the sand is at the surface, forming a substratum which is ordinarily suitable for snails. The absence of all four genera may be due to the inaccessibility of these lakes.

Old Manitou Lake. In this extinct lake, which except for a small area of tamarack swamp is now under cultivation, a boring 9 feet deep revealed no signs of molluscan life. The first 8 feet were peat; then 1 foot of marl; below that, sand (Fig. 4).

Houghton and Moore Lakes. These lakes are north of Old Manitou. Moore is extinct; artificial drainage has greatly reduced the area of Houghton. No living shells were found in either. Fossil shells of Goniobasis were found to a depth of 3.5 feet, and of Campeloma to a depth of 1.5 feet in Houghton

[1] Where such statements are made as "no specimens were found" or "shell-less," they refer to to specimens of the four genera considered in this study. It does not imply that there were no representatives of other genera.

Lake. Both species are represented by fossil shells on the surface of the extinct Moore Lake.

The presence of fossils in these lakes and their absence in Old Manitou, in view of the fact that there is a break in the moraine north of Moore and Hough.ton Lakes, suggests the entrance of Campeloma and Goniobasis into these lakes from the Yellow River.

Maxinkuckee Lake and Its Tributaries. All four species are found living in the lake. A section made in 8 feet of water, north of the railroad pier at Culver, showed 12 feet of marl. In this marl fossil Goniobasis was found to a depth of 8 feet; Pleurocera, 6 feet; Viviparus, 4 feet; and Campeloma, 1 foot (Fig. 4).

In *Lost Lake,* which is a marshy expansion in the outlet of Maxinkuckee, no living shells have been found. A few badly eroded fossil shells of Goniobasis, Pleurocera, and Campeloma were taken from the peat bottom. A boring made about 20 feet out from the northwest shore-line showed the peat to extend to a depth of 3 feet; below this is morainic sand, containing no fossils (Fig. 4). Where the first road crosses the outlet below Lost Lake, a boring was made northwest of the bridge. This shows peat, 6 feet; marl, 1.5 feet, containing fossil Pleurocera and Goniobasis; peaty-marl, 6 inches, containing Goniobasis; shell-less marl, 2 feet; a mixture of marl and blue clay, 1 foot (Fig. 4, No. 1024). About 2 miles south of Maxinkuckee Lake, the Marshall-Fulton County line road crosses the outlet (T32N, R1E, sec. 33). A small colony of living Goniobasis, Pleurocera, and Campeloma was found on the sand on both sides of the bridge. This location marks the upper limit of living colonies in the Maxinkuckee outlet. A mile below another road crosses the stream. This road is a few hundred feet north of the site of a former grist-mill dam. The marshy stream between the two roads supports small colonies of Goniobasis, Pleurocera, and Campeloma wherever the bottom is sufficiently firm. Sections made between the latter road and the mouth of the outlet revealed peat covering sand, without shells (Fig. 4; Nos. 1050, 1051, and 1052).

Eddy Creek. This stream, which is the outlet of Eddy Lake, is dredged throughout its entire course. Careful search in the dredgings revealed no shells, nor was there evidence of any in Eddy Lake. No borings were made.

Nyona and Mud Lakes. These small lakes empty their waters into the Tippecanoe River through Mud Creek Ditch. A few living Campeloma were taken in the sluggish, vegetation-choked lower course of the ditch.

Mud (South Mud) *Lake* contains fossil shells of both Campeloma and Goniobasis. A series of three borings (Fig. 4) on the east shore of the lake at the boat landing shows Goniobasis in the lower layer of the marl deposits where the sand and marl are mixed. Fossil Campeloma were found on the surface. There were no living shells.

In *Nyona* (North Mud) *Lake,* a search for living specimens and a 12-foot boring on the north-east shore gave negative results (Fig. 4).

In *South Mud Lake* there is another instance of Goniobasis living during the early history of the lake, but being exterminated when conditions changed and marl began to accumulate. Artificial drainage probably accounts for the recent extermination of Campeloma.

Manitau Lake Drainage. In about the year 1830 Manitau Lake was formed by the damming of four smaller lakes. The water area is nearly 900 acres (Blatchley, 1902); about half of this area is less than five feet in depth. Although the shallow water area of this lake is extensive, Pleurocera and Goniobasis are confined largely to the northern and eastern littorals. Here Pleurocera averaged about 150 individuals per square meter, and Goniobasis averages about 100 per square meter (September 16, 1927). Campeloma occurs sparsely (about 10 individuals per square meter) wherever the water is less than two feet in depth and the accumulation of vegetal debris is not too great.

Two sections were made at Manitau Lake, both of them along the east shore about 500 feet south of the country club grounds. The first was made in the cat-tail (Typha) marsh about 15 feet from the shore line. At this location there was 3 feet of muck, 1 foot of peat, and then morainic sand; no shells (Fig. 5, No. 1091). The second was made in open water (north of the Typha marsh) about 10 feet from the present shore line. It showed: washed sand, 2 inches; peat, 4 feet; mixed peat and marl, 1.5 feet; granular marl, containing fossil shells of Goniobasis, 1.5 feet; morainic sand (Fig. 5, No. 1092).

Mill Creek, the outlet of Manitau Lake, is shallow and pebbly in its upper course. Here Pleurocera, Goniobasis, and Campeloma were found. On the spillway of the dam at Manitau Lake, Pleurocera and Goniobasis were especially abundant. One count gave 200 individuals of Pleurocera, and 450 Goniobasis in one square meter (September 16, 1928). In the lower course of the outlet near its mouth, where the bottom is a shifting sand, no living shells could be found.

Manitau Lake has two inlets, Mill Creek from the south and White's Creek from the east. The latter, also known as Harrison-Graham ditch, is dredged; it is not inhabited by any snails of the genera under consideration. Mill Creek, however, contains representatives of Goniobasis, Pleurocera and Campeloma throughout its entire course from Manitau to Millark Dam. Just below Millark Dam, where the sawdust from the mill is dropped into the stream, living Campeloma occur in the greatest numbers that the writer has ever seen (about 1,000 individuals per square meter, August 16, 1928).

The nine-foot dam at Millark Mills impounds the water for about two miles in the narrow inter-morainic valley. There are no living shells in this

pond; but a mile upstream from the pond Campeloma was found along the muddy margins of the narrow dredged ditch.

The fact that Campeloma has so successfully maintained itself in Mill Creek and has actually spread to its headwaters, while in all the other tributaries of the Tippecanoe it appears almost to be facing extinction, may be explained by the theory that the maintenance of the water level is the determining factor. The constancy of the water level has been due, of course, to the dams which form Manitau and Millark Lakes. On the other hand, it may be said that these two dams constitute more or less effective barriers to the upstream migration of Campeloma. This inadequate explanation is all that we have to offer to account for the extreme abundance of this species immediately below the dam.

Chippawanuck Creek. Throughout the lower four miles of this dredged stream the only snails that could be found were a few dead Campeloma, about 2 miles from the mouth. The stream was not traced to its source.

Yellow Creek Drainage. This drainage includes Yellow Creek, Mud, Hill, Hammon, McClure, Loon, and Beaver Dam Lakes. This group of lakes lies near the angle formed by the Packerton and Burket moraines (Fig. 3). The area immediately surrounding the lakes is low and marshy, a condition due perhaps to artificial lowering of the lake level by drainage.

Yellow Creek Lake, the lowest lake of the series, is the only one of this group that has any indication of having once been populated by *Viviparidae* and *Pleuroceridae*. One live specimen of Campeloma was taken along the south shore. A few fossil shells of Pleurocera were found along the northern littoral near the outlet. One boring in Yellow Creek Lake and seven in the other lakes of this group are negative for fossils (Fig. 5).

Meredith Ditch, the outlet of this group of lakes, is dredged throughout its entire course; about 11 miles. The dredging has evidently exterminated the snails; only one dead shell of Pleurocera and a few of Campeloma were found.

UPPER COURSE

In the Tippecanoe River north of the Fulton-Marshall County line to Tippecanoe Town, Campeloma, Goniobasis, and Pleurocera occur very sporadically. The stream valley is narrow here and the bottom is sandy. Scarcely any aquatic plants appear in mid-stream. Upstream from Tippecanoe town to the Kosciusko County line, Pleurocera and Campeloma inhabit the muddy margins; Goniobasis is confined mostly to the roots of trees. Above the Kosciusko County line to Atwood, the river meanders through a swamp. Fallen trees and debris so obstruct its course that 12 hours were required to go downstream by rowboat, although the distance by road is only 1.5 miles. Campeloma, Pleurocera, and Goniobasis, though not entirely absent, are so scattered that it was found impossible to collect any considerable

number. From Atwood upstream to Oswego living Campeloma, Pleurocera, and Goniobasis occur; Goniobasis is especially abundant on the Eel-grass (Vallisnaria) in mid-stream. The remainder of the upper course of the Tippecanoe River will be discussed in connection with the lakes which it connects.

Huffman Lake. Dredging the outlet has greatly reduced this lake and exposed large areas of peat and marl. A region north of the present lake which was once a part of it is now under cultivation. A boring made in this region, about one-half mile north of the lake, and an examination of the dredged inlet revealed no shells. One of the striking features of Huffman Lake is the barrenness of its shore and littoral regions, in comparison with most other lakes of the Tippecanoe River system. No living snails occur. A boring made on the middle island of this lake, though probably not presenting a true picture of the history of molluscan life in the lake, is of interest in that fossil Goniobasis were found throughout the entire 29-foot marl boring. They are, however, only about half as abundant in the lower strata as in the upper (Fig. 5, No. 821; also duplicate boring 1053). Another, and probably more typical boring, made on the eastern shore of the lake, at the water's edge, had a depth of 12 feet; Goniobasis occurring to a depth of 8 feet only (Fig. 5, No. 1054). Campeloma is found to a depth of one foot in this, as well as in the two borings on the island. In the dredged outlet vegetation is abundant, and much plant detritus has accumulated. A few living Goniobasis are found on the roots of trees and in scattered small areas of clean loam, but not within one-half mile of the lake. An occasional living Campeloma was also taken from the loam. A few dead shells of Pleurocera were found north of the Pennsylvania Railroad bridge about three-fourths of a mile from the lake.

Palestine Lake Drainage. Palestine Lake has been formed by the damming of Trimble Creek. Its deep water area is small, and a dense growth of vegetation covers the extensive littoral. A boring made in the channel north of the deep water area, in 8 feet of water, showed 9 feet of shell-less marl (Fig. 5).

Two borings (Fig. 5) and a careful search in Caldwell Lake and its outlet, which is the chief tributary to Palestine Lake, yielded no shells.

In Trimble Creek, the outlet of Palestine Lake, dead shells of Pleurocera and Goniobasis are found up to the point where this stream flows through a gap in the moraine (about two miles from the Tippecanoe). Campeloma is found throughout the entire course of the outlet. It does not occur in Palestine Lake, but is abundant immediately below the dam.

Crystal Lake. This lake discharges its waters through a small dredged ditch into Trimble Creek. Along the margin of the lake near the outlet a few living shells of Campeloma occurred. There were no shells in a boring made on the north shore of the lake (Fig. 5).

Goose Lake Chain. It is a peculiar fact that Campeloma occurs in Goose Lake at the head of this chain, although the outlet to this group of lakes is so swampy as to form an effective barrier to the migration of this snail. A 34-foot boring at Sickle Lake, the lowest lake of the chain, failed to demonstrate the presence of fossil shells (Fig. 6).

Muskelonge Lake Group. This group includes Muskelonge, Carr, Little Carr, Fish, Tibbit's and Schultz Lakes. Borings made in all of these lakes give negative results (Fig. 6).

Walnut Creek is the outlet of this group. The upper half has been dredged. No shells were found here, but in the natural stream bed of the lower half dead Goniobasis and Pleurocera and a few living Campeloma were collected.

Winona Lake Drainage. Winona Lake contains colonies of living Goniobasis, Pleurocera, and Campeloma, as well as fossil Goniobasis and Campeloma in its marl deposits. One boring, if taken in the present or former littoral region of a lake, is usually, but not always, sufficient to demonstrate the presence or absence of fossil mollusca. The depth to which fossils occur may vary greatly in different parts of the same lake, as shown by the 12 borings taken in Winona Lake (Fig. 6). No snails were found in the streams and lakes tributary to Winona Lake. Three small streams empty into this lake: Clear Creek, Boy's City Creek (outlet of Stafford and Shelly Lakes), and Eagle Creek (outlet of Smith-Guy, Stoller, Stevens, Sherben, Sellers, and Tennant Lakes). Borings in Stafford, Stoller, and Sherben Lakes were shell-less (Fig. 7). A few living Campeloma and Goniobasis, and an occasional Pleurocera occur in the upper part of the Winona outlet, Scott Ditch. A mile below the lake this ditch joins Walnut Creek, the outlet of the Muskelonge Group. Below the union the stream has been dredged; the Warsaw City sewer empties into it. No shells were living there.

Center Lake. No living shells occur in this lake. Fossils of Goniobasis and Campeloma are abundant, especially along the western and northwestern shores. Goniobasis occurs to a depth of 2 feet in a three foot section made along the southeastern shore (Fig. 7).

Pike Lake. Fossil shells of Pleurocera and Goniobasis are abundant in the sub-littoral zone near the outlet of the lake. These, together with Campeloma, are found in other parts of the lake but not in such great abundance. According to the borings in this lake (Fig. 7), Goniobasis entered this lake first.

Little and Big Chapman Lakes. Goniobasis, Pleurocera, and Campeloma are found living on the marl bottom of both lakes. A boring between the lakes shows Pleurocera in the upper foot, and Goniobasis throughout the marl deposit (Fig. 7, No. 822). In another section, on the eastern shore of

Big Chapman, Goniobasis was the only fossil encountered. It occurred to a depth of 3 feet (Fig. 7, No. 783).

In the outlet, Heter Creek, a few living Campeloma were found about a mile downstream from Little Chapman Lake, and one colony of Pleurocera two miles from the lake.

Oswego Lake. The usual three species are found in this lake. They are confined to the only two areas that have sandy substrata, one near the outlet and another near the inlet. In other places the margins are low and swampy, except along the south shore where the substratum is marl. Only Goniobasis appears in a 3.5 foot section (Fig. 7).

Tippecanoe Lake. The distribution of Campeloma, Pleurocera, and Goniobasis is colonial rather than continuous in this lake. All of them were especially abundant in the southern littoral near the west end of the lake. One boring showed Goniobasis; another, Goniobasis and Pleurocera; while the third made in a former embayment of the lake was shell-less (Fig. 7, Nos. 788, 789, and 1069).

James Lake. This lake is the eastern continuation of Tippecanoe Lake. It contains living Campeloma in small numbers. Fossil Goniobasis and Pleurocera occur in the marl deposits (Fig. 7).

Stanton Lake. The small ditch which connects Stanton and Tippecanoe Lakes is intermittent, so that the two lakes are completely separated for the greater part of the year. Goniobasis is found living. There were no fossils.

Webster Lake. The water level of Webster Lake is maintained by a mill dam in the narrow valley of the outlet. Above the dam on the concrete retaining walls Goniobasis may be taken in large numbers during the latter part of the summer. Small numbers of Campeloma may be found burrowing in the marginal sand. Two borings were made in Webster Lake. One of them showed fossil Goniobasis in the marl. In the outlet Goniobasis and Campeloma thrive. The former is abundant upstream from the highway bridge in Section 15 (T33N, R7E). Pleurocera is found from one-half mile above James Lake up to the Webster Lake dam. Its upstream migration has been halted by the dam and it is not found in Webster Lake above. Two borings were made in swampy ground between this bridge and Webster Lake. The one nearest the stream bed, about 10 feet south from the water's edge, showed fossil Pleurocera and Goniobasis in the 6-inch stratum of marl (Fig. 7, No. 1050). The other, taken 500 feet south of the present stream bed, showed a mixture of sand and gravel below the 6-foot layer of peat (Fig. 7, No. 1051). The gravel and sand layer was heavily laden with fossil shells of Pleurocera and Goniobasis.

"Backwater" of Webster Lake. Certain portions of the "Backwater," where open water occurs, are usually considered as distinct lakes, and given separate names: Black, Greider, Snoke, and Kaiser. No living shells occur

in these lakes. Fossils of Goniobasis were found in the borings of all except Black Lake (Fig. 8).

Mill Pond. No snails could be found in this artificial lake. But immediately below the dam, in the stream that connects Mill Pond with the Backwaters, Goniobasis and Campeloma flourish.

Bauker and Johnson Lakes. These small oval lakes were united before artificial drainage into a single body of water. No living shells occur in them. An occasional dead shell of Campeloma may be taken from the surface of the marl deposits; Goniobasis was found to a depth of 8 feet (Fig. 8). The stream between Bauker and Mill Pond is dredged. No living snails were found in it. In this outlet, two borings were made; one, in the cat-tail marsh not far from Mill Pond, contained no fossils (Fig. 8, No. 1073); the other, near Bauker Lake, contained fossil Goniobasis in a narrow layer at a depth of 9 feet (Fig. 8, No. 1072).

Horseshoe Lake Chain. This lake chain is tributary to Johnson Lake. It includes Horseshoe, Beer, and Brown Lakes. Neither living nor fossil shells occur in this chain (Fig. 8).

Smalley Lake. No living shells occur in Smalley Lake or in the dredged outlet which connects it with Bauker. The lake does contain fossils, as shown by the borings (Fig. 8) made in the Typha marsh on the southwest side of the lake. Fossil Campeloma and Goniobasis were picked up from the surface of the lake bottom.

Gilbert Lake Chain. Little Metz is the lowest lake of this chain. It contains no shells (Fig. 8), nor does Big Metz Lake, a few hundred yards to the north (Figs. 8 and 9).

Buckle, Stump, and *Gilbert Lakes* do not contain living shells, but all of them formerly supported Campeloma and Goniobasis, as evidenced by scattered fossil shells. A boring at Buckle Lake (Fig. 9) showed a layer of mixed marl and sand, containing badly eroded shells of Goniobasis. A 22-foot boring in Gilbert Lake (Fig. 9) contained Goniobasis in the upper 7 feet of marl.

Loon Lake and Its Tributaries. A small colony of Campeloma was found in a small protected area along the southern littoral. A boring in this lake was shell-less. Old, New, and Goose Lakes, which are all tributary to Loon, are entirely barren of shells (Fig. 9).

Dollar Lake. No shells were found in this lake.

Big Lake. A few living Campeloma were taken from the northwestern littoral where the margins are less swampy than elsewhere in this lake. Four marl borings, three of which are shown in Fig. 9, and several pipe probings showed no fossils. The outlet of Big Lake, which flows into Smalley, has been dredged. There was no evidence of living or fossil shells.

Goose, Heriff, and Crane Lakes. These are tributary to Big Lake. None of them contain shells (Fig. 9).

Crooked and Little Crooked Lakes. Crooked Lake contains living Goniobasis and Campeloma but not in any great abundance. Fossil Goniobasis occurs near the surface of the marl. Little Crooked Lake is in reality an eastern embayment of Crooked Lake; it contains Goniobasis and Campeloma in the upper foot of the marl deposits. No shells could be found in the outlet of these lakes, which empties into Big Lake. The introduction of Goniobasis into the Crooked Lakes has evidently been in comparatively recent times, as evidenced by its occurrence near the surface of the deposits only.

Barbee Lake Group. This group includes Sawmill, Plew, Irish, Banning, Shoe, Little Barbee, Big Barbee, Dan Kuhn, and Heron Lakes. Sawmill, the lowest lake in this group, contains fossils only. Two borings (Fig. 10) show Goniobasis occurring to a considerably greater depth than Pleurocera. In the outlet, Grassy Creek, Goniobasis and Campeloma are confined to the small area of gravel and sand just below the bridge. This bridge is near the former site of a mill dam. Plew Lake, which is connected to Sawmill, supports living Goniobasis, Pleurocera, and Campeloma. The first two were found fossil in one of the three borings in this lake (Fig. 10). From Irish Lake, which empties into Sawmill, a few live specimens of Campeloma were taken near the inlet from Little Barbee. No other living shells could be found. Fossils of Pleurocera and Goniobasis were found throughout the 3-foot layer of marl (Fig. 10). Banning Lake is an embayment of Irish Lake. Living and fossil shells are absent from this lake. Shoe Lake drains into Banning Lake. No snails were found here (Fig. 10). Little Barbee Lake empties into Irish, near the outlet of the latter to Sawmill. A few living specimens of Campeloma were found. Goniobasis and Pleurocera occur in the marl deposits (Fig. 10). Big Barbee is connected with Little Barbee by a weed-bordered channel. A few living Campeloma were found along the northern shore, on sand outwash from the base of the moraine. Fossil Goniobasis and Pleurocera are present in the marl (Fig. 10). Dan Kuhn (Kuhn) Lake is an eastern embayment of Big Barbee. There were no fossils in the single boring made in this lake (Fig. 10), but fossil Goniobasis and Pleurocera were picked up along the eastern shore from the surface of the lake bottom. Heron Lake drains into Dan Kuhn. In this nearly extinct lake, no shells occur.

The existence of fossils indicates that snails were formerly living in all the larger lakes of this group. The Sawmill Dam, by changing the water level with comparative suddenness, caused their extinction in Sawmill Lake. Since its removal they have not been able to reëstablish themselves there, but are still living in the lake above (Plew) and in the stream below (Grassy Creek).

Ridinger Lake. A few living shells of Goniobasis and Campeloma were taken along the northeast shore on the gravel substratum. Two borings made near an abandoned marl pit showed fossil Goniobasis (Fig. 10). The outlet of Ridinger Lake (Grassy Creek) empties into Big Barbee. A boring made in a former embayment, near Ridinger Lake, was shell-less (Fig. 10, No. 615); another made farther downstream, about 1.3 miles from Big Barbee Lake, yielded Goniobasis and Pleurocera in the upper 2 feet of the marl (Fig. 10, No. 1048).

Robinson and Rine Lakes. No snails were found in Robinson Lake, either living or fossil, in the 8-foot boring made in the marl pit on the northwest side of the lake (Fig. 10). Rine Lake is also shell-less. In the outlet of Robinson Lake near its confluence with the outlet of Big Cedar, one dead specimen each of Campeloma and Goniobasis were the only shells found.

Tadpole Lake. No evidence of snails were found in this lake, which drains into the outlet of Big Cedar Lake.

Big Cedar Lake. A few living shells of Campeloma were taken from the sandy margins along the eastern shore of this lake. No evidence of fossils were found in the deposits along the southern shore. The outlet of this lake joins the outlet of Robinson Lake near the Kosciusko-Whitley County line about 1 mile north of Robinson Lake.

Little and Big Mud Lakes. These two lakes, northern tributaries of Big Cedar Lake, are in reality only small open-water areas in a tamarack bog. Both are shell-less.

DISCUSSION AND SUMMARY

It is evident that the fossil mollusca in the Tippecanoe deposits are postglacial, since the Tippecanoe drainage itself was established during the late Wisconsin substage of glaciation (Malott, 1922; Leverett, 1915). The absolute depth to which fossils occur in the deposits is not important for the purposes of this study, since the rate of deposition of marl varies in different localities; but the relative depth of the different species in the same boring is significant, since it shows the relative length of time each species has existed in that locality. The fact that *Goniobasis livescens* occurs to a greater depth than any of the other species is evidence that it was the first to enter this river system. Similar evidence shows *Pleurocera acuta* to have entered next, and finally came *Campeloma rufum.* In Maxinkuckee Lake, *Viviparus contectoides* appeared before Campeloma.

To determine the routes of migration into the Tippecanoe River system, the physiography of the region must be taken into account. Dryer (1893:22-28) and Mallott (1922:118) consider the Packerton morainic system to have been largely of Saginaw origin (Fig. 3). The erie lobe of the Wisconsin glaciation is considered younger than the Saginaw lobe. By the time of Erie

glaciation, the Saginaw had probably retreated far enough to establish most of the upper course of the present Tippecanoe drainage system. The middle course of the Tippecanoe was ponded (Glacial Lake Kankakee). The major migration from the west into the middle course probably took place at this time. It was this migration from the Iroquois and Kankakee Rivers through Glacial Lake Kankakee that supplied the original stock of Goniobasis, Pleurocera, and Campeloma which has since spread throughout most of the Tippecanoe River system. Minor migrations have also occurred from the north.

Aside from physiographic conditions making this interpretation most probable, evidence for this major migration from the west is as follows: (1) No living or fossil shells are found below the village of Pulaski, either in the Tippecanoe River or its tributaries (except Campeloma, within a short distance of the mouth of the river); hence, these species very evidently did not enter the Tippecanoe primarily from the Wabash. (2) There have been several minor migrations into the Tippecanoe River System, but each of these migrations affects only one lake or group of lakes. The distribution is in no case continuous with that in the remainder of the Tippecanoe system. The fact that these minor migrations can be clearly demonstrated makes the occurrence of a similar migration from the west quite probable.

The minor migrations into the Tippecanoe River system have been from the north into (1) Maxinkuckee Lake, (2) Houghton and Moore Lakes, and (3) the Gilbert Lake group.

Maxinkuckee forms of Goniobasis, Pleurocera, Campeloma, and Viviparus have been introduced from the Yellow River. The following facts suggest this interpretation: (1) fossils are found in the marl deposits of Lake Maxinkuckee and in the upper part of its outlet; (2) fossils are not found in the lower part of the outlet (near the Tippecanoe River) (3) a marshy area on the crest of the Maxinkuckee moraine (T32N, R1E) is drained by tributaries of both the Yellow River and Maxinkuckee Lake. The order in which these snails entered Maxinkuckee Lake as evidenced by the depth to which they occur in the marl borings is Goniobasis, Pleurocera, Viviparus, and Campeloma.

The migration of Goniobasis and Campeloma into Houghton and Moore Lakes has evidently been from the Yellow River also. Their absence in Old Manitou Lake (south of the lakes under discussion) and the sluiceway, extending north from Houghton and Moore Lakes toward the Yellow River, point to this conclusion.

Goniobasis and Campeloma have been introduced into Gilbert, Buckle, and Stump Lakes from the Elkhart drainage through the Indian Village chain of lakes. This conclusion rests upon the following facts: (1) Fossil shells of Campeloma and Goniobasis are found in Bouse Lake (the upper lake of the Elkhart drainage), and also in Gilbert, Buckle, and Stump Lakes. (2)

Neither living nor fossil shells of Campeloma or Goniobasis occur in Big and Little Metz Lakes. If these snails had migrated into Gilbert, Buckle, and Stump Lakes from the Tippecanoe drainage (via Smalley Lake, through Little and Big Metz), there should be some fossil evidence in the Metz Lakes. Careful search shows that this is not the case. (3) A low ridge separates the Metz Lakes from Gilbert, Buckle, and Stump. An artificial dredged ditch through this moraine forms the present outlet of the Gilbert group of lakes. A swampy, channel-like depression between the Indian Chain and the lakes in question is evidence that drainage was formerly into the Elkhart River.

The extent of distribution within the river system varies greatly in the different species, and is not necessarily proportional to the depth to which the same species occur in the marl deposits. In other words, the rate of dispersal has been different for each of the four species.

Campeloma, although it entered last, is the most widely distributed within the Tippecanoe River system, if both fossil and living forms are taken into account (Fig. 13). It occurs throughout the entire course of the river, except between Pulaski and the Oakdale Dam. The upstream limits of distribution of the original stock in the tributaries are in Bruce Lake, South Mud Lake, the inlet of Manitau Lake, Yellow Creek Lake, Huffman Lake, the outlet of Palestine Lake (below the dam), the outlet of Muskelonge Lake (about half a mile from the lake), Winona Lake, Center Lake, Pike Lake, Chapman Lakes, Robinson Lake, Cedar Lake, Johnson Lake, Loon Lake, and Crooked Lakes.

Goniobasis is the second most widely distributed (Fig. 11). It occurs in the Tippecanoe River from Pulaski upstream to Smalley Lake. In the tributaries the upstream limits of the original stock occur in Bruce, the inlet of Manitau, Huffman, the outlet of Palestine, the outlet of the Muskelonge group, Winona, Center, Pike, Chapman's, and Ridinger Lakes.

Pleurocera is somewhat more restricted than Goniobasis (Fig. 12). Its lower limit of distribution in the Tippecanoe River coincides with that of Goniobasis; upstream, it occurs as far as the Webster Lake Dam. In the tributaries, the original stock terminates in the inlet of Manitau Lake, the outlet of Palestine Lake, the outlet of the Muskelonge Group, Winona Lake, Center Lake, Pike Lake, the Chapman Lakes, and the inlet of the Barbee Group.

The presence of living Goniobasis in Crooked and Little Crooked Lakes and its absence in nearby lakes (Big and Crane) are difficult phenomena to explain except as cases of accidental distribution. The writer's first theory was that Goniobasis came into these lakes from Cedar Lake of the Eel River drainage. But a careful search revealed no specimens of Goniobasis, either living or fossil, in Cedar or any other lakes of the Shriner group. On the other hand, it is not likely that this species entered the Crooked Lakes through

the Tippecanoe system, since it is absent from the lake immediately below Crooked (Big) Lake. This is the only case, in the Tippecanoe River system, where the evidence is lacking to show a continuous orderly migration which accounts for present distribution.

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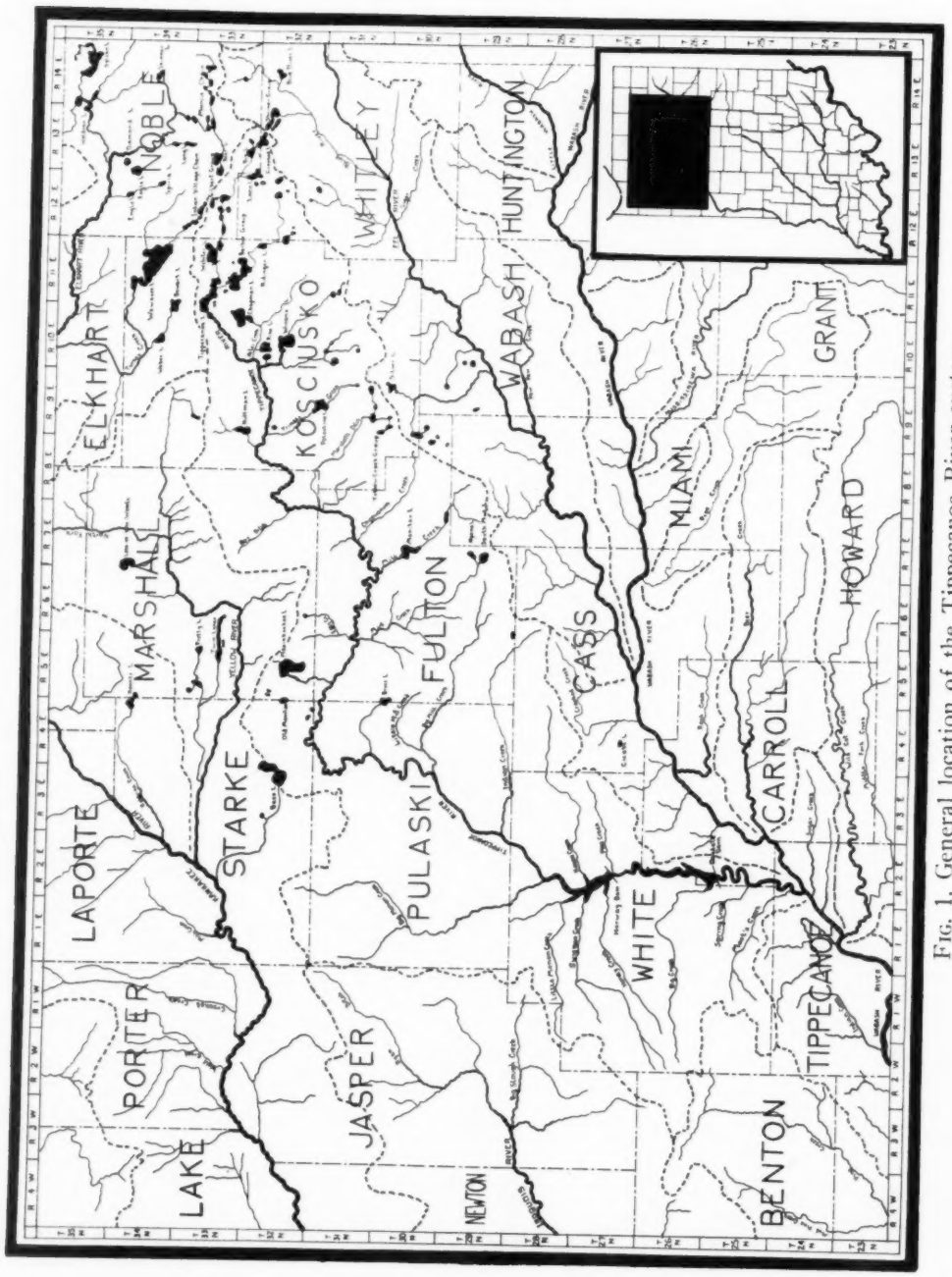


FIG. 1. General location of the Tippecanoe River system.

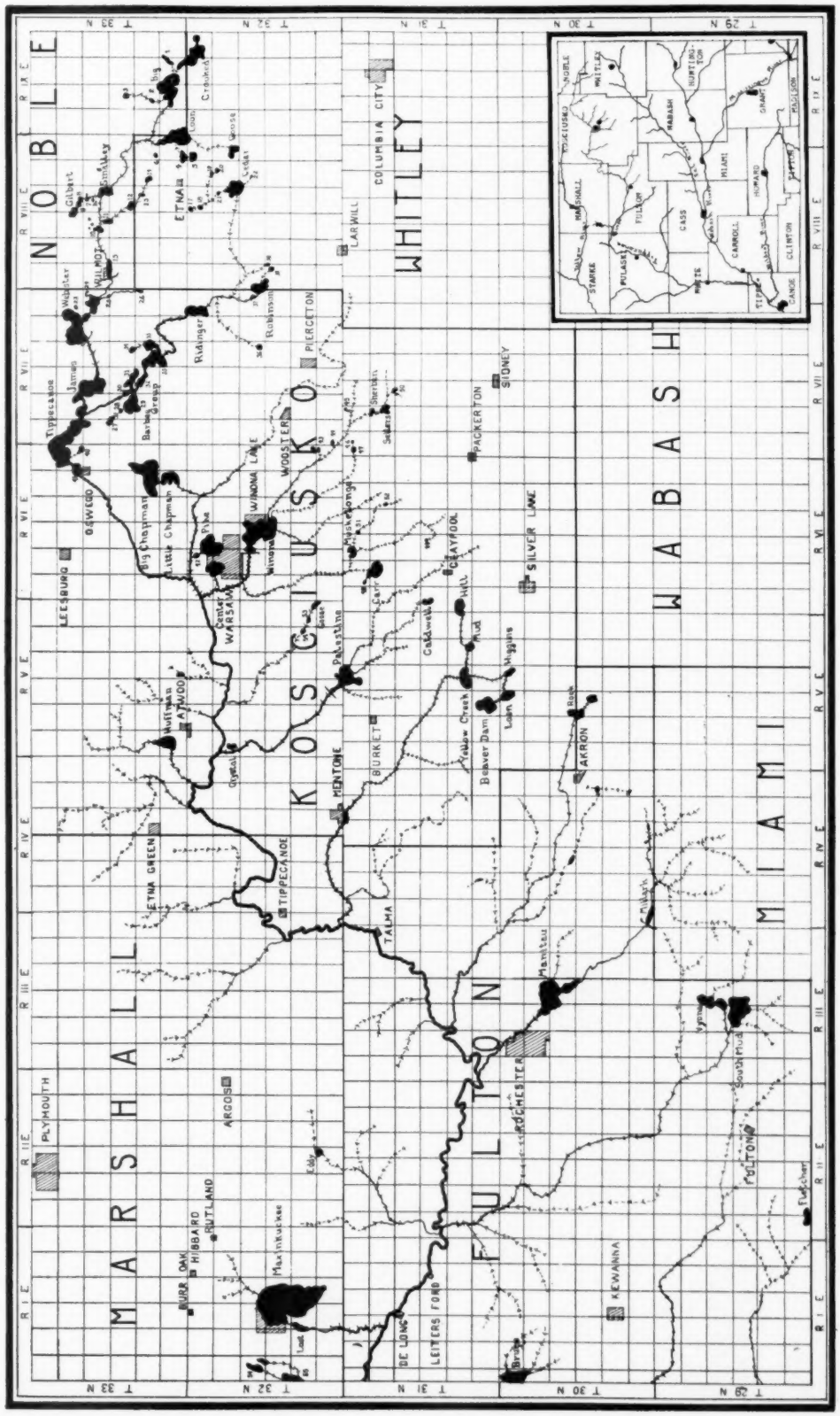


FIG. 2. Lakes of the Tippecanoe system.

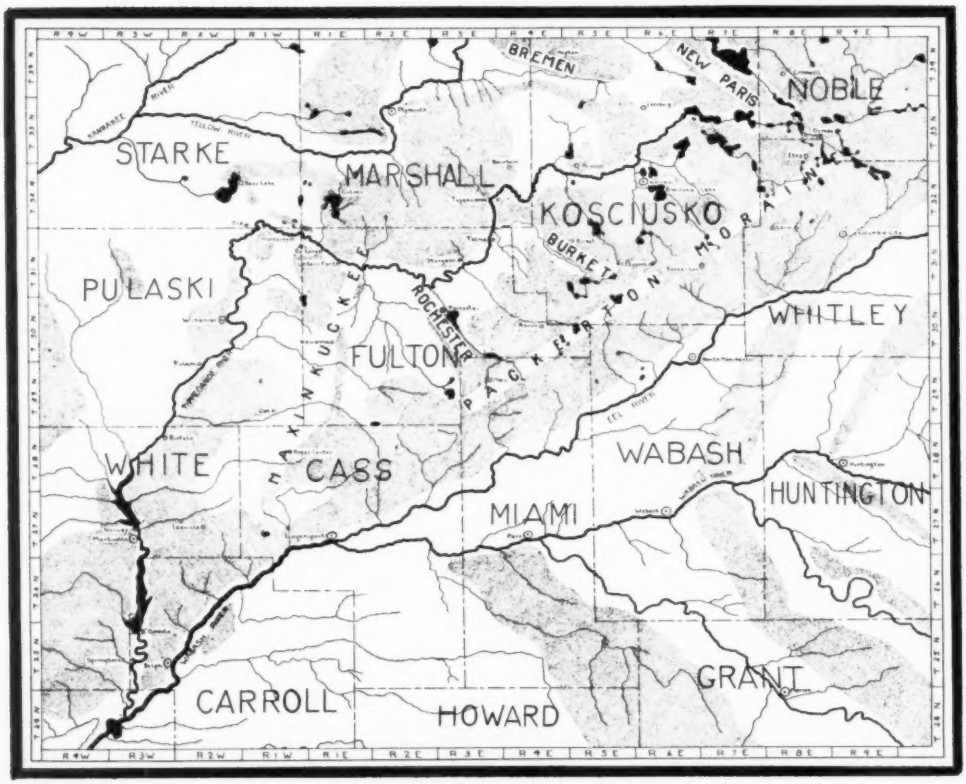
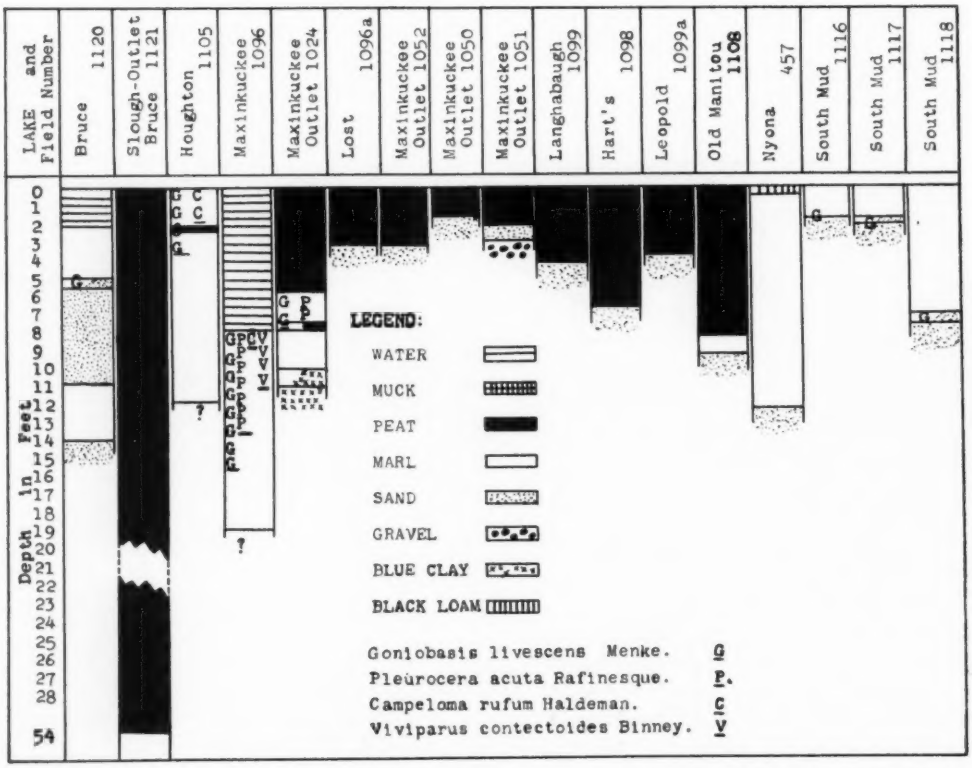


FIG. 3. Moraines of the Tippecanoe region.



FIGS. 4-10. Records of borings in lacustrine deposits showing distribution of materials and fossil shells.

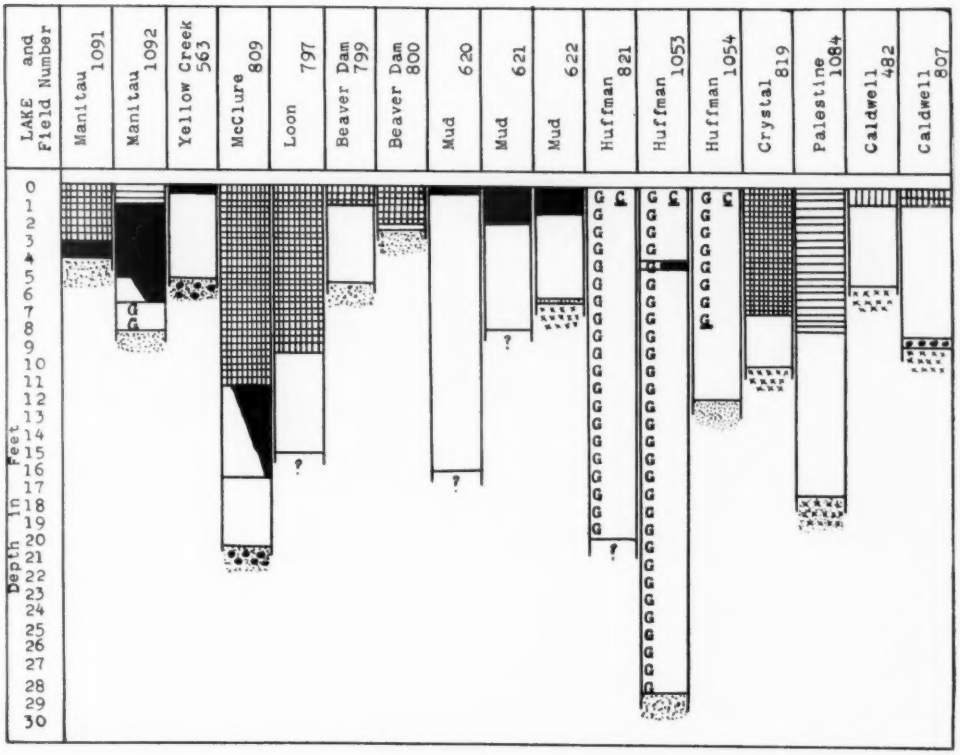

LAKE and Field Number
Manitau 1091
Manitau 1092
Yellow Creek 563
McClure 809
Loon 797
Beaver Dam 799
Beaver Dam 800
Mud 620
Mud 621
Mud 622
Huffman 821
Huffman 1053
Huffman 1054
Crystal 819
Palestine 1084
Caldwell 482
Caldwell 807
Depth in Feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

FIG. 5

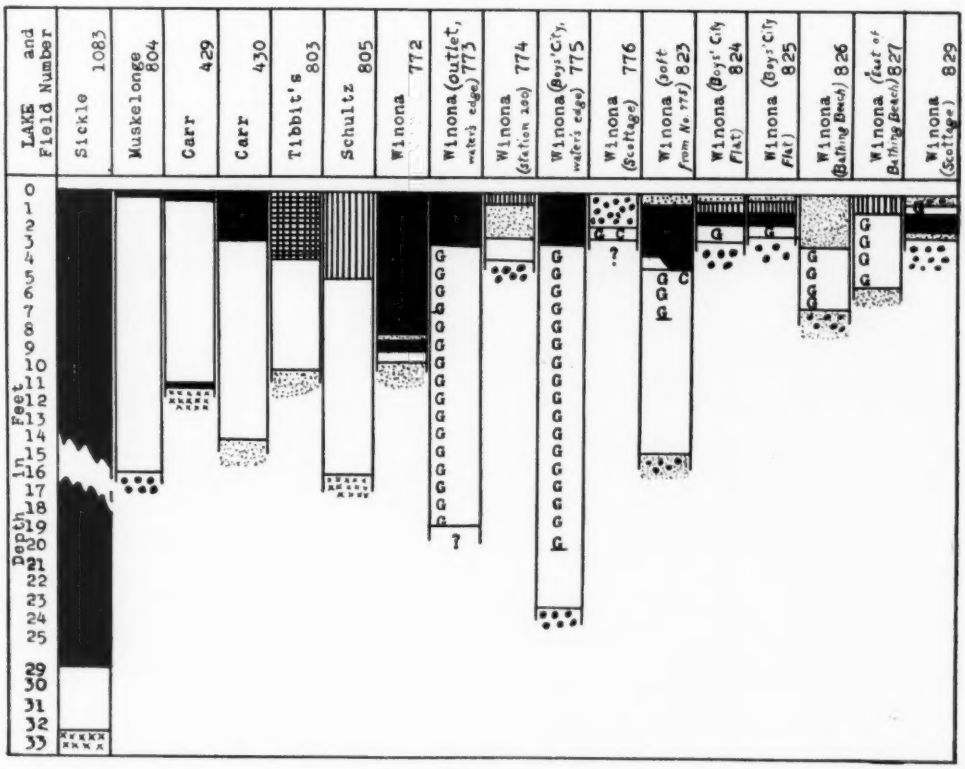

LAKE and Field Number
Sickle 1083
Muskelonge 804
Carr 429
Carr 430
Tibbit's 803
Schultz 805
Winona 772
Winona (outlet, waters edge) 773
Winona (station 200) 774
Winona (Boys' City, waters edge) 775
Winona (Scottage) 776
Winona (soft from No 776) 825
Winona (Boys' City Flat) 824
Winona (Boys' City Flat) 825
Winona (Bathing Beach) 826
Winona (East of Bathing Beach) 827
Winona (Scottage) 829
Depth in Feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 29 30 31 32 33

FIG. 6

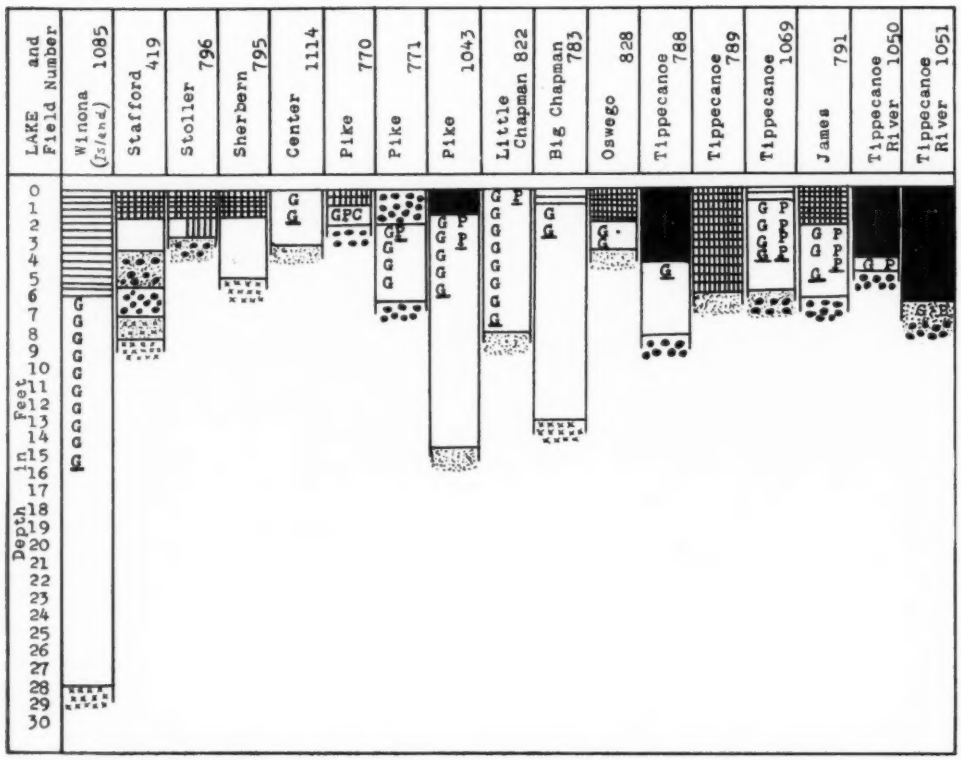

LAKE and Field Number
Winona (Island) 1085
Stafford 419
Stoller 796
Sherbern 795
Center 1114
Pike 770
Pike 771
Pike 1043
Little Chapman 822
Big Chapman 783
Oswego 828
Tippecanoe 788
Tippecanoe 789
Tippecanoe 1069
James 791
Tippecanoe River 1050
Tippecanoe River 1051
Depth in Feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

FIG. 7

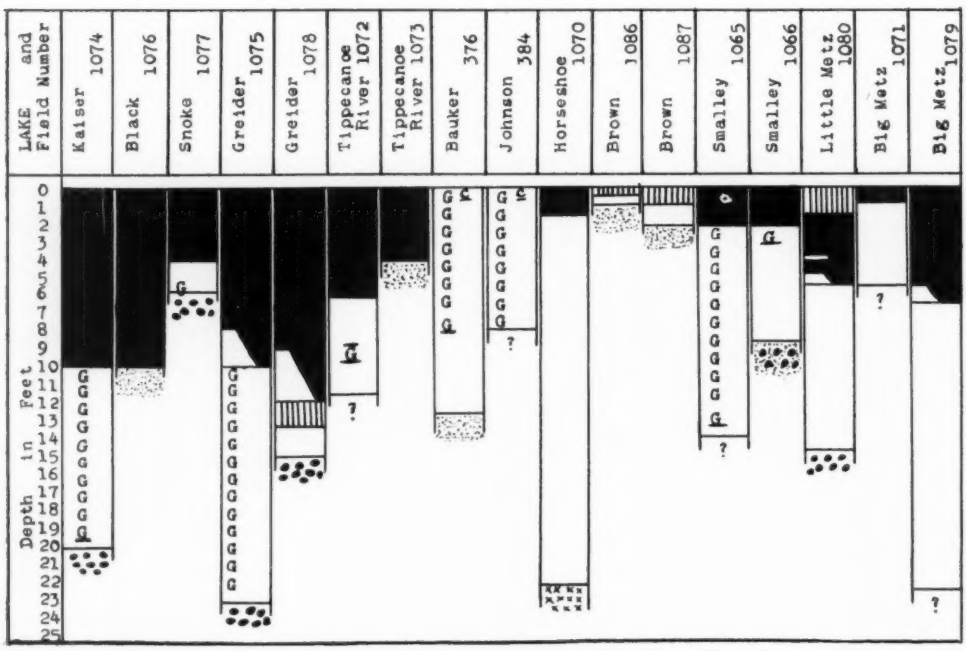

LAKE and Field Number
Kaiser 1074
Black 1076
Snoka 1077
Greider 1075
Greider 1078
Tippecanoe River 1072
Tippecanoe River 1073
Bauker 376
Johnson 384
Horseshoe 1070
Brown 1086
Brown 1087
Smalley 1065
Smalley 1066
Little Metz 1080
Big Metz 1071
Big Metz 1079
Depth in Feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25

FIG. 8

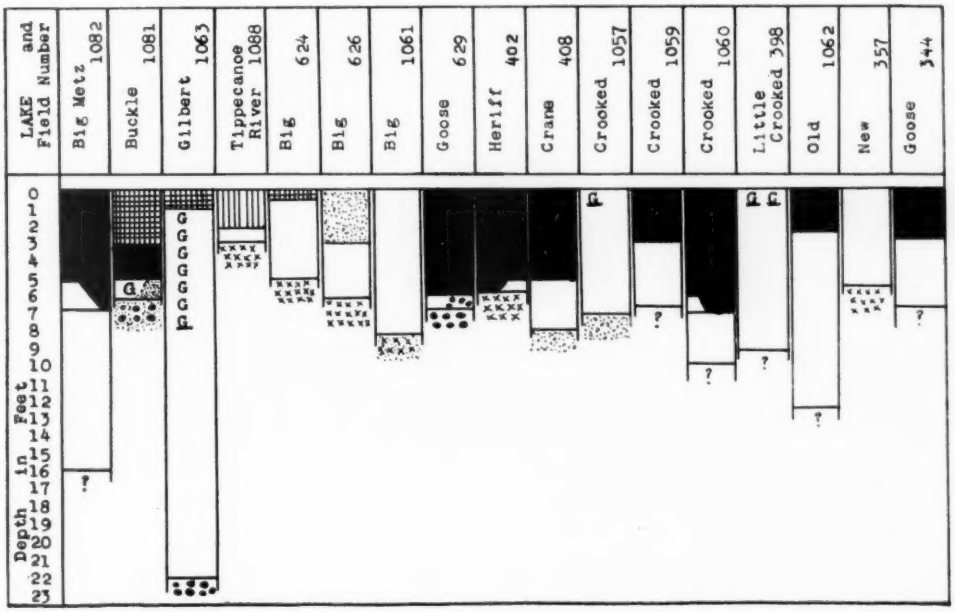

LAKE and Field Number
Big Metz 1082
Buckle 1081
Gilbert 1063
Tippecanoe River 1088
Big 624
Big 626
Big 1061
Goose 629
Heriff 402
Crane 408
Crooked 1057
Crooked 1059
Crooked 1060
Little Crooked 398
Old 1062
New 357
Goose 344
Depth in Feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

FIG. 9

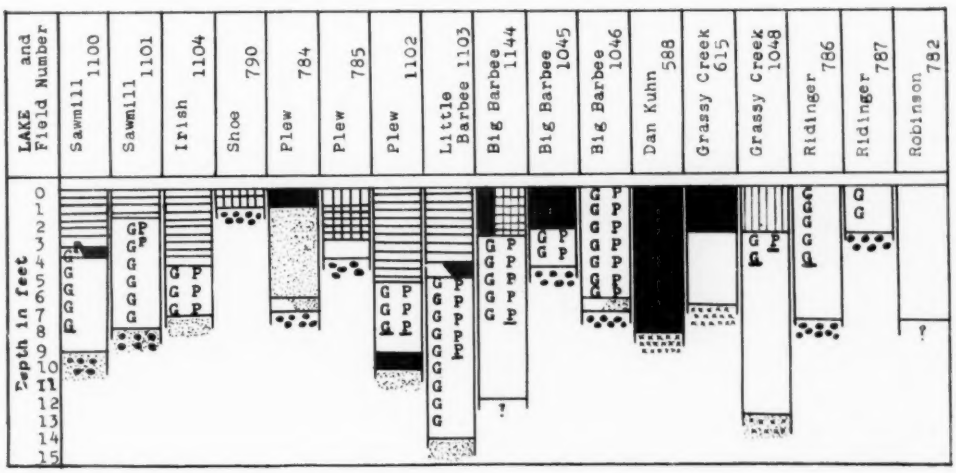

LAKE and Field Number
Sawmill 1100
Sawmill 1101
Irish 1104
Shoe 790
Plew 784
Plew 785
Plew 1102
Little Barbee 1103
Big Barbee 1144
Big Barbee 1045
Big Barbee 1046
Dan Kuhn 588
Grassy Creek 615
Grassy Creek 1048
Ridinger 786
Ridinger 787
Robinson 782
Depth in feet
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15

FIG. 10

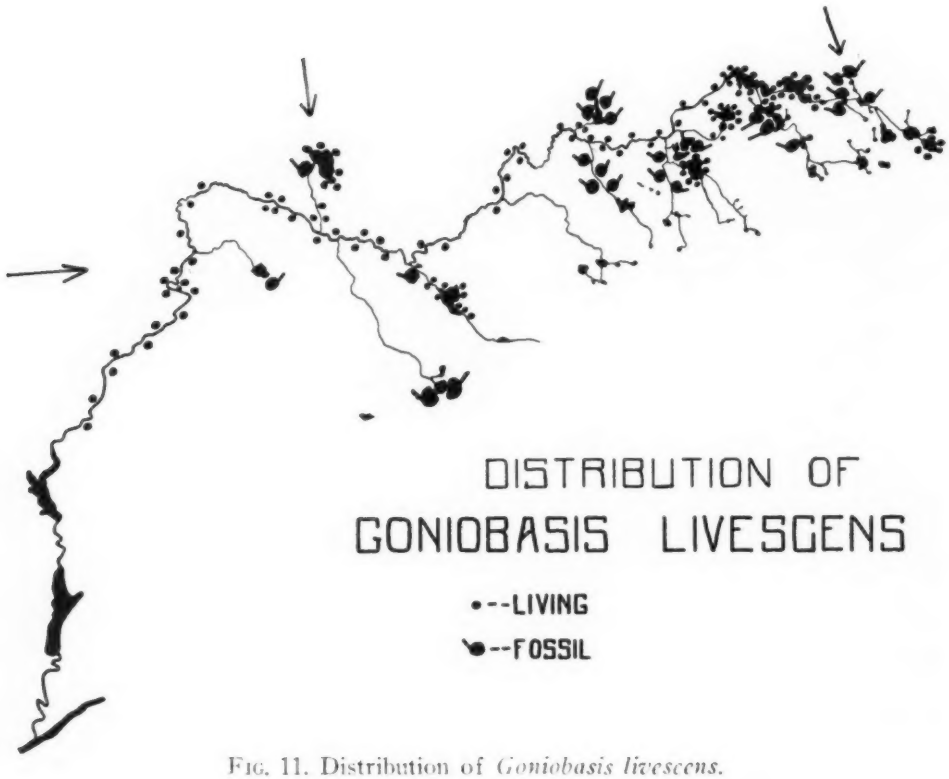


FIG. 11. Distribution of *Goniobasis livescens.*

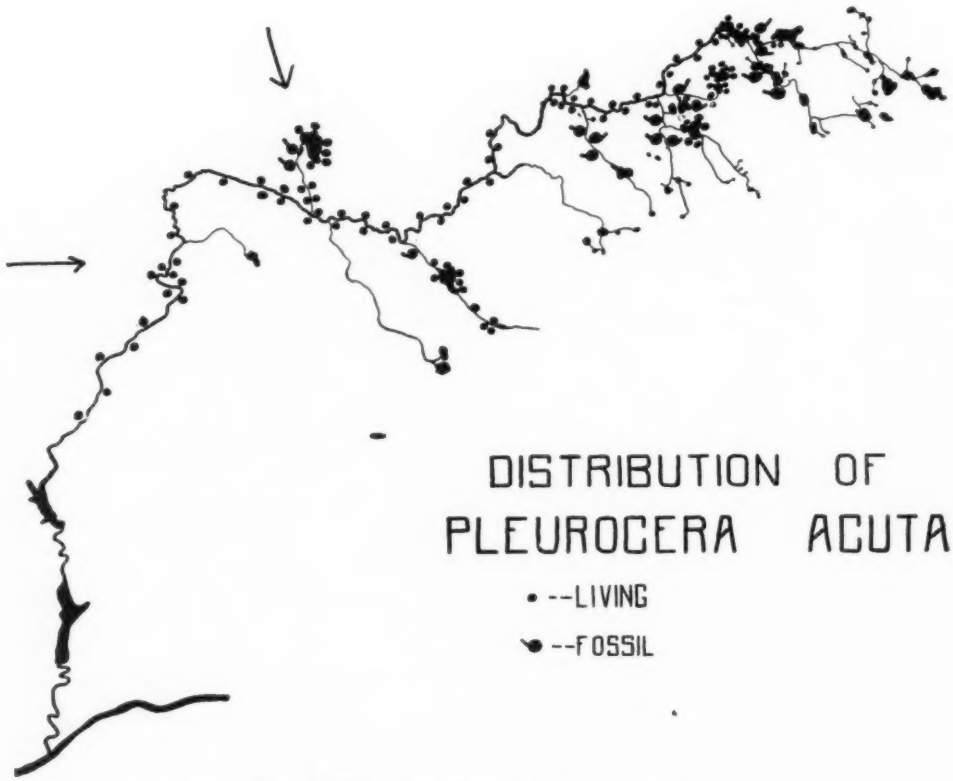


FIG. 12. Distribution of *Pleurocera acuta.*

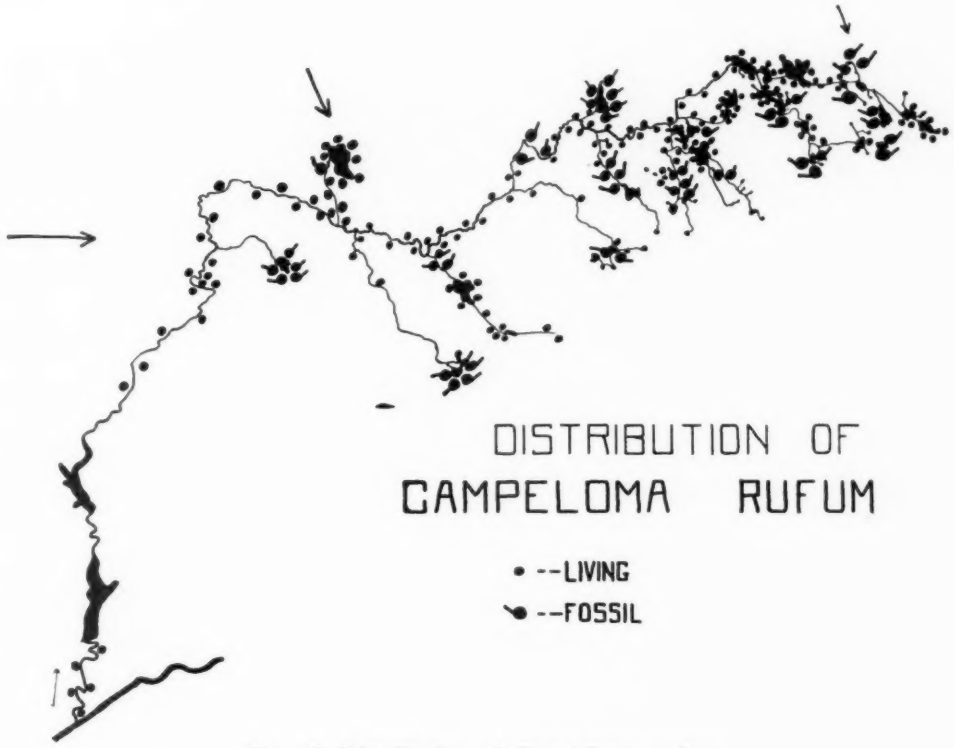


FIG. 13. Distribution of *Campeloma rufum*.

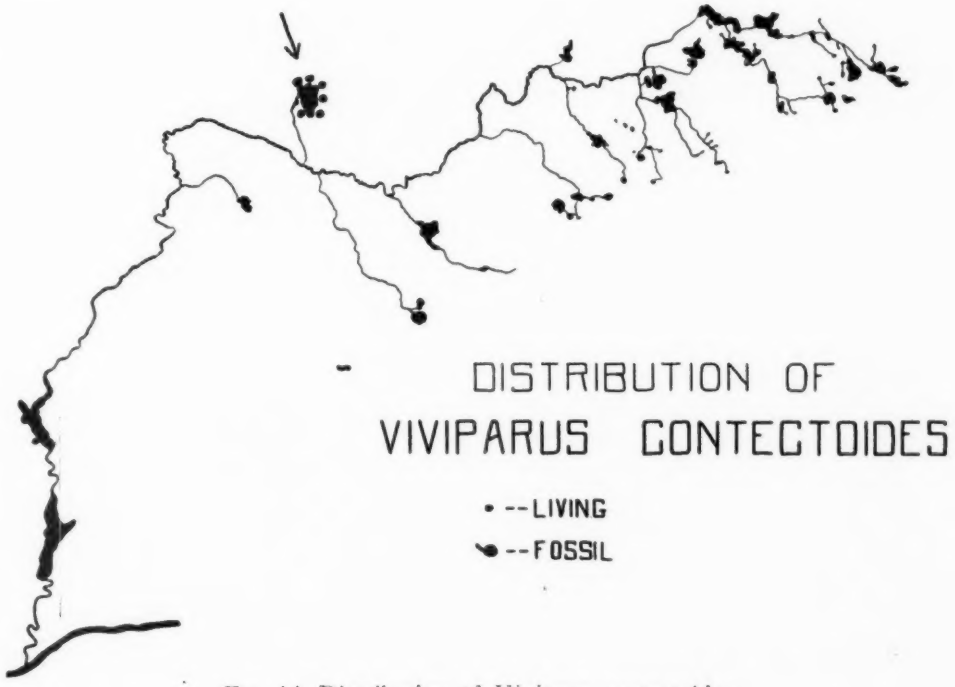


FIG. 14. Distribution of *Viviparа contectoides*.

AN EXPERIMENTAL STUDY OF THE GROWTH OF POPULATIONS OF THE "FLOUR BEETLE" *TRIBOLIUM CONFUSUM* DUVAL, AS AFFECTED BY ATMOSPHERIC MOISTURE

By

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AN EXPERIMENTAL STUDY OF THE GROWTH OF POPULATIONS OF THE "FLOUR BEETLE" *TRIBOLIUM CONFUSUM* DUVAL, AS AFFECTED BY ATMOSPHERIC MOISTURE

INTRODUCTION

The problems at present facing the entomologist demand more and more an understanding of the relation of environmental factors to insect abundance. That physical factors play a part has long been recognized; that biotic factors are also important is common knowledge; but that there may be special physical conditions which must act in close association with the biotic factors for the satisfactory functioning of the latter is a phase of applied entomology which is not so widely realized. The present study is primarily concerned with the direct relation of a physical factor, atmospheric moisture, to experimental populations of the "flour beetle," *Tribolium confusum* Duval. The results, however, have indicated that the physical factor may have its expression, in part, through a resultant indirect biological effect.

Of the physical factors which play a part in insect activity, no doubt heat, as measured by temperature, has received more attention than have the others. Its effects, particularly in extremes, force their attention very strikingly on the observer. However, water is perhaps the most important of the constituents of living protoplasm, as it is essential for all life processes. On its regulation depends the economy of living organisms. Atmospheric moisture as rain affects this economy in animals directly and indirectly through soil and plants. The effects of atmospheric moisture as humidity are less evident and as a result may have been considered of less importance. It is natural then, that temperature in relation to biological phenomena should have had more attention centered on it than has moisture. It is also probable that the difficulties associated with maintaining constant conditions of humidity in spaces large enough to permit of experimental work on biological processes, have to some extent been responsible for retarding studies in this direction. Payne (1929) has recently shown that some of the phenomena attributed to the action of temperature are as much (if not more) associated with humidity as with temperature. It is thus evident that greater recognition of the importance of atmospheric moisture to insect life is already showing itself.

At present there are three main methods of expressing the moisture conditions of the air: (1) as relative humidity, (2) as absolute humidity, and (3) as saturation deficiency. The question as to which of these is the most suitable when dealing with ecological phenomena is still far from settled. Botanists are inclined to consider "saturation deficiency" as the most satisfactory, as far as plant problems are concerned, since it is the evaporating

power of the air which is important (Bolas, 1926; Blackman, 1929; Buxton, 1930). On the other hand most references to humidity in both botanical and zoölogical literature are given in terms of "relative humidity." When taken in conjunction with temperature such a measure has proved very useful for expressing the relation of air moisture to certain biological phenomena, as for example the survival of grasshopper eggs recorded by Parker (1930) and also cited in Chapman's (1926) "Animal Ecology." In these cases neither absolute humidity nor saturation deficiency expresses the relation any better.

In recent years there has been a tendency for certain zoölogists, more particularly investigators of plague, to consider moisture conditions in terms of saturation deficiency (Brooks, 1917; Hirst, 1927; Pirie and Murray, 1927). Nevertheless both Brooks and Pirie and Murray point out that saturation deficiency cannot be considered alone without temperature, although with perhaps less consideration of temperature than is necessary when the records are given as relative humidity. Payne's (1929) results on the relation of humidity to winter hardiness of tussock moth eggs indicate that "vapour pressure" is the most satisfactory method of expressing atmospheric moisture, there being a straight line relationship between it and winter hardiness. Actually in her paper Payne uses the expression "absolute humidity" but the data quoted indicate that it is really vapour pressure which she is considering. Close examination of her results shows that at any *particular* temperature either relative humidity or saturation deficiency gives a close correlation with the winter hardiness effect, but only at that particular temperature. The relation between the two, however, does not show a straight line correlation in the case of Japanese beetle larvae.

At present one cannot go further than say that it is probable that no single method of recording atmospheric moisture will be applicable to all aspects of insect activity over all ranges of temperature. The two factors are intimately associated and until a more critical study of the situation is made it will be necessary always to record both temperature and humidity at the same time. Ultimately it will probably be found that one method may be more satisfactory for consideration of certain types of phenomena than for others, or for certain ranges of temperature than for the total range, or else that a new form of expression must be sought. Further it must be borne in mind that if the effect of atmospheric moisture on biological phenomena lies in its relation to the evaporation power of the air, even an expression which gives a relatively uniform relation between humidity and the particular phenomenon cannot be expected to be without variation in every case, unless the other conditions which contribute to affect the evaporation power of the air are controlled or otherwise allowed for; for atmospheric moisture, while a very important factor in determining the evaporation power of the air, is only one of several.

HUMIDITY AS A FACTOR IN INSECT ENVIRONMENT

Records of the effect of atmospheric moisture on insects, especially those of economic importance, usually have reference to its effects on some particular stage or activity of the insect, and indicate that the amount of atmospheric moisture present may be of considerable importance in its life processes.

Bachmetjew (1907), summarized the effect of humidity as follows: (1) There is an optimum moisture for insect development. (2) The optimum is not the same for different species. (3) Moisture which may hasten development of one species may retard development of another. As early as 1894 Giard in drawing attention to "anhydrobiose" or the slowing down of vital phenomena under the influence of "déshydration," mentioned examples from the Insecta; later he recorded a similar retardation of development in the Diptera (1896, 1902, and the Hymenoptera, 1896). Marchal (1907) observed the effect of reduced humidity in prolonging the larval or pupal stage of the pear cecidomyid (*Diplosis pirivora* Riley). Willcocks (1916) in Egypt, has noted the great acceleration to emergence of adults from "resting larvae" of the pink bollworm (*Pectinophora gossypiella* Saund.) given by an increase in the relative humidity. Pierce (1916) has represented graphically the relation between humidity, together with temperature, and activity of the boll weevil (*Anthonomus grandis* Boh.). His diagram is perhaps rather idealistic, nevertheless it calls attention to the subject in a manner which will undoubtedly have application in numerous cases. It also shows in a very striking way how extremes of atmospheric moisture may constitute limiting factors to an insect's activity. Headlee (1913, 1914, 1917, 1918) has done pioneer experimental work on varying conditions of humidity in relation to insects. As a result of studies on the grain moth (*Sitotroga cerealella* Oliv.), the bean weevil (*Bruchus obtectus* Say.) and the grain louse (*Toxoptera graminum* Rondani) he has drawn attention to the wide variation in the effects of humidity on different stages of an insect, and on different species. Although Headlee found little effect of different relative humidities on the aphid, Toxoptera, Davidson (1921) found an effect of atmospheric moisture on *Aphis rumicis* Linn. He had difficulty in rearing it "in the warm dry atmosphere of the laboratory," whilst "in a similar temperature in the humid atmosphere of the greenhouse they developed normally."

Buxton (1924) has recorded an interesting relation between the activity of desert insects and humidity through the hygroscopic property of certain dried desert plants. At night the plant material absorbed water from the air and this was used by the insects as a source of moisture. Shelford (1913) studied the reactions of various animals, including insects, to changes in evaporating power of the air, resulting from different humidities. More recently (1927, 1929) he has considered the evaluation of the effect of relative

humidity together with that of temperature on the codling moth in terms of "developmental units." Rudolfs (1925) has observed the effect of humidity on the activity of mosquitoes, and Cook (1920) has shown its relation to the flight of Noctuid moths. Hefley (1928) has made an important and interesting study on the differential effects of relative humidity on the Hawk Moth (*Protoparce quinquemaculata* Haworth.) and one of its parasites, and Weese (1924) has noted the effects of different humidity conditions on a spider and its hymenopterous parasite. In connection with her studies on the "blow-fly," *Lucilia sericata* Meign., Cousin (1929) has drawn attention to the importance of atmospheric moisture on the life processes of this fly and in particular on its relation to the "diapause" or suspended activity in that insect. McCulloch (1923) found that hatching of Hessian fly eggs rarely takes place at relative humidities below 60%, while at such conditions if hatching is successful the newly hatched larvae are unable to crawl on to the stems of the host plant. In this case there appears to be a relation between the dryness of the stem and the inability of the larvae to maintain themselves there. Holdaway (1927) has shown the relation between atmospheric moisture as a factor in the evaporation power of the air and seasonal activity of the Collembolan *Smynthurus viridis* Linn. and Davies (1928) has studied experimentally the differential humidity requirements of this and other species of Collembola.

The writer's own interest in humidity and its relation to insect activity and abundance was first aroused by an observation on the pentatomid bug, *Tectacoris lineola* Fab. (1926) a pest of cotton in Queensland.[1] It was found that if the relative humidity was low at the normal time for pairing, mating did not take place, and the eggs laid were infertile. If, however, the relative humidity rose during the interval between normal mating and oviposition, sexual activity was immediately aroused and fertile eggs resulted.

Many more examples of the relation of humidity to insect life could be found, but sufficient should now have been cited to indicate both its importance and the variety of ways in which its effect is manifest. Its most important aspect is undoubtedly in its relation to the water content of the organism. Even though the response of an insect to external conditions lead to much of the free water in its tissues being transformed to bound or colloidal water (Robinson, 1928, 1928a, 1928b, 1928c) nevertheless, as Robinson has shown, this characteristic varies considerably in different species and although serving as a safety measure cannot be infallible as a means to survival under extreme conditions even with species able to conserve their water content by the faculty of binding a very large proportion of the water present

[1] These observations were made on bugs reared from hatching in large screen cages over cotton plants in the field. The insects in a state of sexual activity are easily recognizable. Moreover since they congregated at sunset and remained quiescent during the night, it was possible by regular observations while the sun was shining to note the approach of sexual activity without fear of its escaping attention.

The importance of regulation of the moisture content of living organisms has been considered in general works. In insects the phenomenon has been studied by Berger (1907) in Tenebrio and Bodine (1921) in grasshoppers. Further, inhibition of water is one of the most important aspects of growth (Davenport, 1899; MacDougall, 1920; Gortner, 1929). But if metabolism is limited by the relative humidity of the atmosphere to the *maintenance* of moisture content apart from *increase,* then growth is prevented and may even become negative. In such a case relative humidity would constitute a limiting factor of growth. Berger (1907) found that Tenebrio larvae kept in dry air and fed on dry food maintained their moisture content but lost weight. That atmospheric moisture is very important in determining ability to survive, has been shown by Barnes and Grove (1916), who found that survival of grain weevils, particularly at high temperatures, was greater in moist atmospheres. Beattie (1928) found that adults of the "blow fly," *Calliphora erythrocephala,* survived higher temperatures with the humidity at 70 per cent, the thermal death point being lowered by saturated or dry air.

Although the regulation of the moisture content in insects is important, the percentage present is not constant in all stages nor does the absolute amount always increase throughout life. There is evidence that a reduction in moisture content takes place at pupation (Bataillon, 1893). Bodine (1923) with grasshoppers and Heller (1926) with Lepidoptera have shown that there is a reduction in moisture content during hibernation. If this state of affairs is a common accompaniment of dormancy, one can understand more fully the necessity of adequate moisture conditions in assisting the cessation of hibernation which has been found in so many cases—in grasshopper eggs by Parker (1929), with codling moth larvae by Townsend (1926), with grasshoppers by Bodine (1923), cotton flea hopper by Reinhard (1928), pink boll worm by Willcocks (1916), mosquito eggs and European corn borer by Rouboud (1926, 1928) and with the boll weevil by Hunter and Pierce (1912).

It has long been known that the temperature of the so-called "cold blooded animals" approximates to that of their environment. It is now known, however, that, notwithstanding this approximation, quite a range of variation exists between the body temperature and that of the environment, in both invertebrate and vertebrate poikilothermic animals. For example, it has been found in many cases that under low moisture conditions the temperature of an insect's body is lower than that of the environment. The explanation of this state of affairs often given is that the reduction in temperature is due to a cooling effect resulting from evaporation (Dutrechet, 1840; Buxton, 1924; Necheles, 1926). This explanation is undoubtedly incomplete. The writer has briefly studied the temperature of eggs of Tribolium in connection with the environmental temperature when development takes

place at different humidities; and while the temperature of the eggs developing in the drier atmosphere was lower than that of the eggs in the moister condition, the difference was not such as would be expected from the difference in evaporating power of the air at the two conditions. Also it has been calculated that the decrease in temperature brought about and maintained over a certain period of the development could not be due to cooling by evaporation. The loss of water would have been so great as to exceed the total amount present. The real explanation will probably be arrived at through a consideration of the heat exchanges associated with the internal water relations which are affected by the external environment, together with a consideration of the effects of respiration.

One more effect of atmospheric moisture will be mentioned briefly. During the course of the studies to be discussed in the succeeding pages, it was found that the sex ratios of adults derived either from parents or from eggs which had been maintained at respectively different moisture conditions were different. The point has been mentioned already in brief (1930), and will be treated in greater detail in a subsequent publication (1932?). Suffice it to say that the change in sex ratio is no doubt due to sex reversal, since it has been found that sex can be reversed as late in life as the larval stage by other environmental conditions. In this connection it is of interest to recall Mahdihassan's (1924, 1926) results on the change in sex ratio of lac insects according to moisture conditions associated with the season.

Each of the above-mentioned cases indicating the effect of humidity on an insect is an exceedingly interesting observation on the relation of atmospheric moisture to some phase of an insect's physiology, and would have an effect on the ultimate numbers, of the particular species, surviving. Little attention has, however, been given to this latter aspect of humidity research and the effect of humidity on insect populations. The present study was therefore begun from a slightly different view point from those previously cited. Its aim was to consider the effect of atmospheric moisture on the insect from the point of view of the growth of a population in a unit environment, regardless, in the first place, of its effect on any particular phase of the insect's physiology.

GROWTH PHENOMENA IN GENERAL

The phenomenon of growth has been studied in a wide variety of living forms and from several points of view, from populations of yeast cells to human populations, and from the growth of plants to the growth of man himself.

As long ago as 1845 Verhulst, a Belgian, in studying human populations conceived the idea of representing growth phenomenon mathematically and in graphic form. Since that time growth has been studied in a great variety of living organisms. Brown, A. J. (1892, 1905), Brown, H. T. (1914), Clark

(1922), and Richards (1928) have studied the growth of yeast cell populations; Fawcett (1921) the increase in diameter of mould colonies; Roach (1926) the increase in soil algae; Anderson (1895) the growth of fruits; and Reed (1920, 1921, 1928) the growth of plants, portions of plants and rats. Robertson (1921, 1923) has studied experimental populations of infusoria; Durbin (1909) the rate of regeneration of tadpoles' tails; Donaldson (1915) and Robertson (1926) the growth of rats; Knibbs (1928) human populations; and Pearl (1925, 1927, 1928) a variety of forms including plants, and both insect and human populations. The works of D'Arcy Thompson (1917), Robertson (1923), Pearl (1925), Lotka (1925) and Buchanan and Fulmer (1928) summarize a great deal more work on growth that is not mentioned above.

The results of all these studies have shown that both in individuals and in populations, there is initially a slow growth, followed by a rapid increase, which, after a period of more uniform growth, decreases until a state of comparative equilibrium is reached.[2] Graphically this state of affairs is represented by a "sigmoid" curve. In certain cases of apparent departure from this generalization, it has been shown that the growth curve can be resolved into consecutive "growth cycles" each of which adheres closely to the general form of a separate sigmoid curve. Various examples of such "growth cycles" are given by Robertson (1923). Reed (1928) has demonstrated them in the growth of cognate shoots of lemon trees, and Pearl (1925) and Knibbs (1928) in human populations.

Although an understanding of the growth of insect populations, the magnitude of their oscillations about a mean, their increase to pest proportions and their decrease, are problems of paramount importance to the entomologist, very few attempts have yet been made to study insects experimentally from the basic standpoint of insect numbers. In this connection the work of Pearl (1922, 1925) and Pearl and Parker (1922) with populations of Drosophila and that of Chapman (1928) with Tribolium are almost unique. From a more purely mathematical standpoint considering either insects or living organisms in general are the studies of Thompson (1922, 1924, 1927) and Volterra (1928); while from the point of view of stimulus from the wider field of animal ecology, Elton's (1927) treatise is a land-mark.

Chapman (1928) has demonstrated experimentally with Tribolium that under constant environmental conditions, regardless of the initial population of beetles and the size of the environment, the population eventually comes to an equilibrium, which in terms of a unit environment, as for example one gram of flour, is constant. He has therefore shown in a most striking way, that the tremendous potentiality possessed by Tribolium in common with other

[2] It may be an oscillating equilibrium, particularly in the case of populations, when it is usually possible to arrive at a mean equilibrium provided the time period is sufficiently large.

insects, for the production of an almost limitless population, is never realized. While this has been established for yeast cell populations and other forms of life, it was necessary to demonstrate it for Tribolium if further experimental study on the effect of various factors, physical and biotic, was to be undertaken.

THE EFFECT OF ATMOSPHERIC MOISTURE ON THE GROWTH OF TRIBOLIUM POPULATIONS

TECHNIQUE

The technique used was that developed by Chapman (1918, 1928) in which a given weight of flour was used as the immediate environment of the beetles. The adults normally do not fly. On one occasion only have they been observed by the writer to fly or attempt to fly. This was during the first few minutes in which they were submitted to high temperatures which later resulted in their death. The populations thus can be kept in open glass containers, such as those shown in Fig. 1, which were 10 c. m. in diameter and 5 c. m. deep.

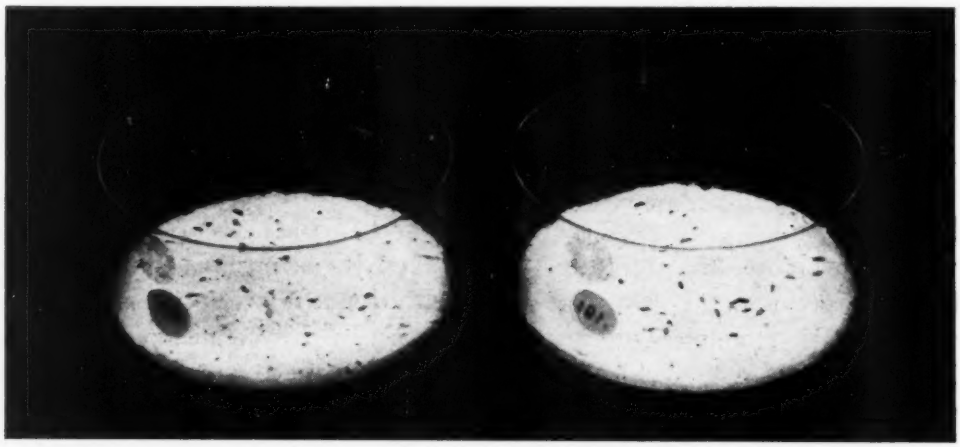

FIG. 1. Experimental populations of the flour beetle, *Tribolium confusum* Duval.

In each of the population studies mentioned in the present paper 20 grams of flour were used; this, when spread over the bottom of the container, had a depth of about 0.5 c. m. Every opportunity was thus given for the flour to be kept in equilibrium with the environmental moisture, rather than some other humidity dependent on the presence of the beetles.

In order to avoid any possibility of variation due to differences in nutritional value from different supplies of flour, sufficient flour was milled specially from whole wheat so that 95% would pass through a number 8 silk bolting cloth.[3] This flour thus constituted a standard nutrient medium of

[3] The wheat was first milled twice in an ordinary experimental flour mill. The siftings were then re-milled separately in a ball mill until most of the flour had reached the

approximately 100% whole wheat. In the light of Sweetman and Palmer's work on the nutrition of *Tribolium confusum* (1928) published after the initiation of these studies, it appears that the precaution to secure a standard medium of approximately 100% whole wheat flour, may have been unnecessarily exacting. For these workers found, for example, that the insect's vitamin B requirement was more than satisfied by the addition of 5% of wheat embryo to a basal ration.

The work was carried out in electrically and compressed air driven conditioning cabinets for maintaining constant temperature and humidity. Cabinets were maintained at 27° C, and at 25%, 50% and 75% relative humidity respectively.

Although populations were developed only at the above-mentioned humidities the effects of humidity on the various stages were also studied in a dry atmosphere (1% ± relative humidity) and at saturation (99% ±). For obtaining these conditions use was made of the fact that in a cabinet maintaining a relatively dry atmosphere, 25% or 50% relative humidity, it was a comparatively simple matter to further dry the air by means of concentrated sulphuric acid to 1% relative humidity, and in a cabinet maintaining a moist atmosphere such as 75% relative humidity, it was a relatively simple matter to further increase the humidity to saturation (99%) by passing the air through consecutive containers of distilled water. The manner in which the cabinets were operated assisted greatly in securing these extra humidities and allowed general population studies to be continued in the cabinet proper, while small subsidiary experimental chambers at different humidities were set up inside the large cabinets. These smaller experimental chambers being inside the large cabinets were thus maintained at the same temperature as the large cabinet (27° C.). In the cabinets used, air was circulated from a row of nozzles in the top, by means of an electric fan. By plugging one of these nozzles with a cork and delivery tube sufficient pressure of air was secured to overcome the resistance of a series of chemical solutions or distilled water as the case may be. That is, instead of air being drawn through the solutions by suction as is usually the case, air was driven through by pressure, tapped off from the general air-circulating current of the cabinet. Thus in a cabinet maintaining a temperature of 27° C. and a relative humidity of 25% or 50%, it was possible to secure additional small experimental chambers inside the large one, at 1% relative humidity by passing the air stream through concentrated sulphuric acid in the usual way. In order to avoid the possibility of acid fumes passing into the experiment chamber, a tube containing granulated soda-lime was inserted between the second sulphuric acid container and the experiment chamber, the series being as follows:

desired fineness. My thanks are due to Dr. C. H. Bailey of the Division of Biochemistry, and to Dr. A. L. Strand of the Division of Entomology, for assistance in preparing this standard flour.

1. C. P. conc. H_2SO_4.
2. C. P. conc. H_2SO_4.
3. Soda lime.
4. Experimental chamber (1% relative humidity).
5. C. P. conc. H_2SO_4 (trap).

If a humidity of 25% was desired at the same time, use was made of the fact that at 27° C. air in contact with a concentrated solution of calcium chloride is maintained at 25% relative humidity (Headlee, 1921; International Critical Tables, 1927). The dry air emerging from the experimental chamber of the first series was passed through an additional series of containers as follows:

1. Conc. solution C. P. $CaCl_2$.
2. Conc. solution C. P. $CaCl_2$.
3. Experiment chamber (25% relative humidity).
4. Conc. solution C. P. $CaCl_2$ (trap).

As previously stated, for securing a saturated atmosphere air in a cabinet at 75% relative humidity was passed through distilled water. The series was as follows:

1. Distilled water.
2. Distilled water.
3. Experiment chamber (saturated atmosphere).
4. Distilled water (trap).

In all cases in which air was passed through a liquid for the purpose of changing its humidity, the delivery end of the air-conducting tube was tapered so that the air bubbles were reduced in size. By adjusting the depths to which the tubes projected in the fluids and by regulating the pressure, the air stream was slowed down so as barely to constitute movement. By thus slowing down the air current, and by reducing the size of the air bubbles every facility was afforded for the air to reach the required humidity before entering the experiment chamber.

In each case in which small subsidiary experimental chambers, such as have just been described, were set up, all corks used were of rubber. After assembly the inlet and outlet tubes were closed and the whole system allowed to come into equilibrium with the temperature of the cabinet at 27° C. The air stream was started a short time before the equipment was required for use.

Population counts of all stages present were made at intervals of ten days, and during the period in which adults were emerging, the pupae and adults were counted also at five day intervals. These stages, and with them large larvae, can be removed from the flour by means of a metal sieve. All other stages were removed by re-sieving the flour with a No. 7 silk bolting cloth. Chapman (1918) found that occasionally a very young larvae was able to pass through this mesh. However, after trials, it was found that with

the continual movement of the flour and the small amount to be sieved, all stages were retained by the No. 7 mesh. As the flour had previously passed through the finer No. 8 mesh, the separation of the insects from the flour was thus facilitated by using a No. 7 cloth.

The flour was removed every ten days at the time the complete population counts were made. In all the populations studied, the equivalent of 20 grams of flour, dry weight, was used; it was necessary to use the dry weight of flour as a unit, since Bailey (1920, 1927) has shown that flour absorbs different amounts of water at different humidities. The weight of flour is thus to some extent a function of the environmental humidity and must be referable to some standard, of which the best is undoubtedly the equivalent dry weight. Table I gives the actual relationship at the humidities at which population experiments were carried out.

TABLE I. *The relation of flour weight to humidity.*

Dry Weight, grams	Relative Humidity, %	Equivalent weight at different humidities, grams
20	25	20.8
20	50	21.9
20	75	22.8

Flour was placed at the required humidity for at least a week prior to being used in order that it might reach a moisture equilibrium. On days on which population counts were to be made the required amount of flour (20.8, 21.9, or 22.8 gms.) according to the relative humidity was weighed out to receive the population as it was counted. The food supply was thus kept constant as regards unit dry weight, quality, and moisture content throughout the studies. At each count the major portion of the flour still remained in the containers with the populations, but a fresh supply was always used, the old being discarded with moulted skins and excreta. By keeping the food supply constant in every possible respect, food was never allowed to enter into consideration as a limiting factor.

THE GROWTH OF POPULATIONS UNDER CONSTANT HUMIDITY CONDITIONS

The stock used was the progeny of about 200 beetles collected in a flour mill. Observations indicated the presence, in small numbers, of the mite *Acrophenax tribolii* Newsted and Duvall (1918) which attacks the eggs of Tribolium. If eggs are removed from the flour within a day of being laid, infested eggs are usually detectable a day or two afterwards. In order to secure cultures, therefore, eggs were removed from the flour daily and each batch examined daily until hatching occurred. All infested eggs were destroyed before the mites had matured, and therefore before the uninfested

eggs had hatched. The Tribolium larvae hatching from the clean eggs were used to secure a clean stock culture.

Populations were developed in duplicate at 25%, 50%, and 75% relative humidity respectively. From the point of view of these experiments carried out at the same temperature (27° C.), it is immaterial whether the moisture conditions be referred to as relative humidity, vapour pressure, saturation deficiency or absolute humidity, since at a constant temperature the relative humidity bears a straight line relationship to each of the other expressions. For the purpose of comparing each of the above methods of expressing atmospheric moisture Table II has been prepared from the United States Weather Bureau Psychrometric Tables compiled by C. F. Marvin (1915) in English units.

TABLE II. *Psychrometric data for the conditions at which experiments were performed. Barometric pressure, 30.0 inches; saturation pressure, 1.042 inches.*

Dry Bulb Temp. (°F.)	Wet Bulb Temp. (°F.)	Relative Humidity (% Sat.).	Vapour Pressure (Inches).	Saturation Deficiency (Inches).	Absolute Humidity (Grains).
80.6°F.	50.6	1±	0.013	1.029	0.011
(=27°C)	59.1	25	0.261	0.781	2.784
"	67.5	50	0.525	0.517	5.569
"	74.5	75	0.797	0.245	8.354
"	80.6	99±	1.042	0.000	11.127

By plotting relative humidity against each of the other expressions the relationships will readily be seen. However, since at present it is impossible to say which method of expressing atmospheric moisture is most satisfactory for ecological purposes, for reasons of simplicity of expression moisture conditions will be referred to throughout this paper in terms of relative humidity.

The initial population in each of the population experiments consisted of 5 males and 5 females emerged the day the experiment was started. The concentration was thus .5 beetle per gram of flour. The populations at 50% and 75% were continued until several readings indicated that an equilibrium had been reached. Those at 25% when nearing an equilibrium, were placed at 75% relative humidity, to note a possible change in growth of the population due to a change in humidity.

Table III gives the means of two populations developed at 75% relative

TABLE III. *The growth of a population at 75% relative humidity and 27° C., the mean of two populations.*

Days	Eggs	Larvae	Pupae	Adults	Total
0	..	..	..	10	10
10	89	0	0	10	99
20	214	94	0	10	318
30	186	254	0	10	450
40	105	314	56	10	486
45	...	...	121	27	...
50	123	201	137	91	553
55	...	...	101	176	...
60	181	102	80	230	592
65	...	...	50	265	..
70	330	69	15	297	712
75	...	...	22	300	...
80	402	32	17	306	757
85	...	...	8	311	...
90	505	40	3	302	852
100	472	69	0	294	835
110	540	66	5	295	892
120	723	53	7	298	1080
130	718	72	3	298	1098

humidity and 27° C. The data are represented graphically in Fig. 2, the numbers of each stage present being plotted separately.

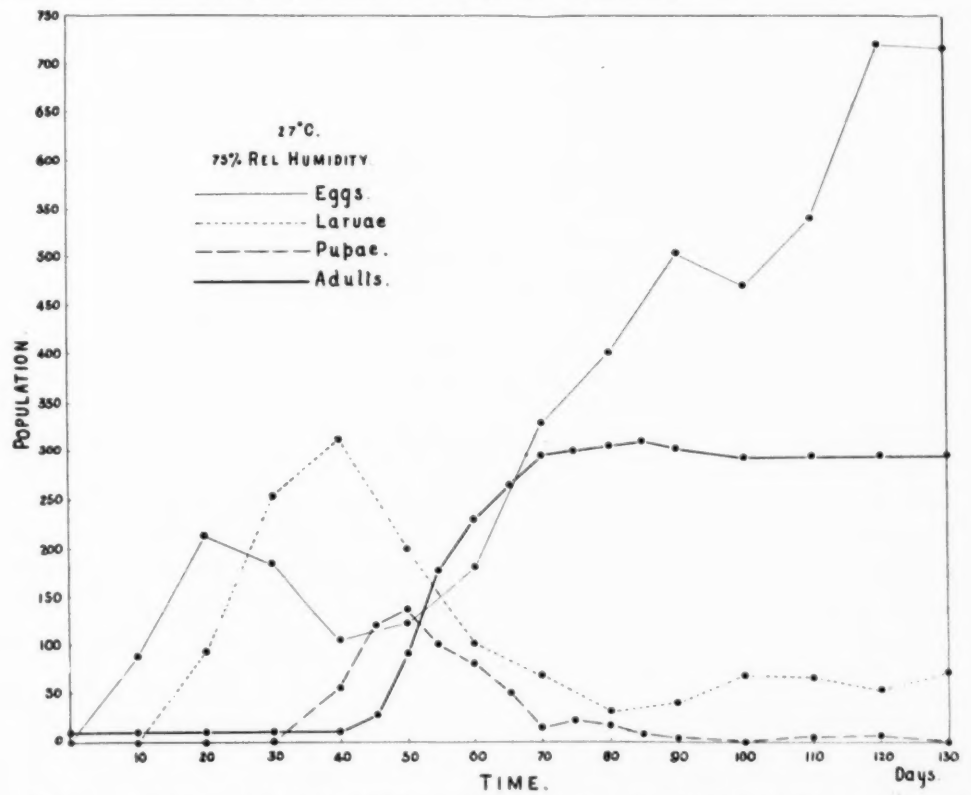

FIG. 2. The growth of a population at 75% relative humidity and 27° C. Mean of two populations. The numbers of each stage present are plotted separately.

It will be seen that at 75 days the adult population had reached a concentration which with slight variations remained uniform and was still at the same magnitude 130 days after the beginning of the experiment. Thus for 60 days it had been at a mean concentration of 300 beetles, or 15 per gram. It will be noted that at 130 days the larval and pupal populations were low while the egg population was high. These facts will be referred to again later.

Table III and Fig. 2 for populations at 75% relative humidity represent the same general state of affairs that occurred in the development of populations at other relative humidities. Data for populations at 50% are given in Table IV and those for a relative humidity of 25% up to 70 days in Table V and Fig. 4. The differences were quantitative rather than qualitative, as can be seen by a comparison of Fig. 2 and Fig. 4, and by an examination of Fig. 3 which shows the adult populations at 25%, 50% and 75% relative humidity respectively.

TABLE IV. *The growth of a population at 50% relative humidity and 27° C; the mean of two populations.*

Days	Eggs	Larvae	Pupae	Adults	Total
0	..	..	..	10	10
10	97	..	..	10	107
20	187	84	..	10	281
30	152	216	..	10	378
40	118	318	19	10	460
45	...	...	80	10	...
50	96	254	119	49	517
55	...	...	103	120	...
60	205	188	59	182	634
65	...	...	44	208	...
70	298	112	27	212	647
75	...	...	33	219	...
80	504	48	26	223	800
85	...	..	26	226	...
90	607	18	7	230	872

A COMPARISON OF THE GROWTH OF POPULATIONS AT DIFFERENT HUMIDITIES

By developing comparable populations at each of three different relative humidities it has been found that environmental moisture plays an important part in both the rate of development of populations and the magnitude of the equilibrium reached. The readings for the growth of adult population at each relative humidity studied, are given in Table V and in Fig. 3.

TABLE V. *The growth of populations (adults) at different relative humidities. Constant temperature of 27° C. throughout. Records for each humidity are the mean of two populations.*

Days	25%	50%	75%
0	10	10	10
10	10	10	10
20	10	10	10
30	10	10	10
40	10	10	10
45	10	10	27
50	13	49	91
55	53	120	176
60	118	182	230
65	162	208	265
70	...	212	297
75	..	219	300
80	...	223	306
85	...	226	311
90	...	230	302
100	...	...	294
110	...	...	295
120	...	...	298
130	...	...	298

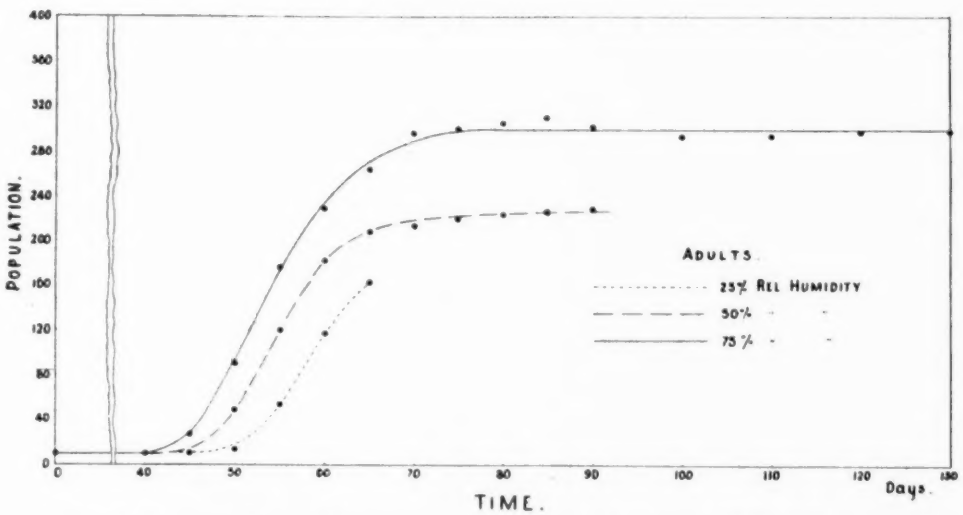

FIG. 3. A comparison of the growth of adult populations at 25%, 50% and 75% relative humidities. All at a constant temperature of 27° C.

As has been stated previously the populations at 25% were removed before an equilibrium was reached, but the trend indicates that they would have come into equilibrium at a concentration lower than that of the 50% population, probably in the vicinity of 190 beetles. The equilibria established are shown in Table VI.

TABLE VI. *Equilibria of adult populations at different humidities.*

Relative Humidity, %	Equilibrium Population	Population per gram
75	300	15
50	227	11.4
25	190*	9.5*

*Approximate.

The population at 50% was continued by Dr. Chapman for an additional 160 days beyond the 90 days at which my observations ceased. I am therefore indebted to him for a more accurate figure for the equilibrium population than my data to 90 days could have furnished. It will be seen that the equilibrium population is a function of the humidity. However, although the equilibrium population increases with increase in atmospheric moisture to 75%, it decreases to zero at saturation, for development of population is impossible under such conditions, owing to the development of fungi. The condition of atmospheric moisture leading to a maximum population, and, as will be seen later, no doubt also to a maximum rate of population growth, thus lies between 75% and saturation, probability in the vicinity of 85%.

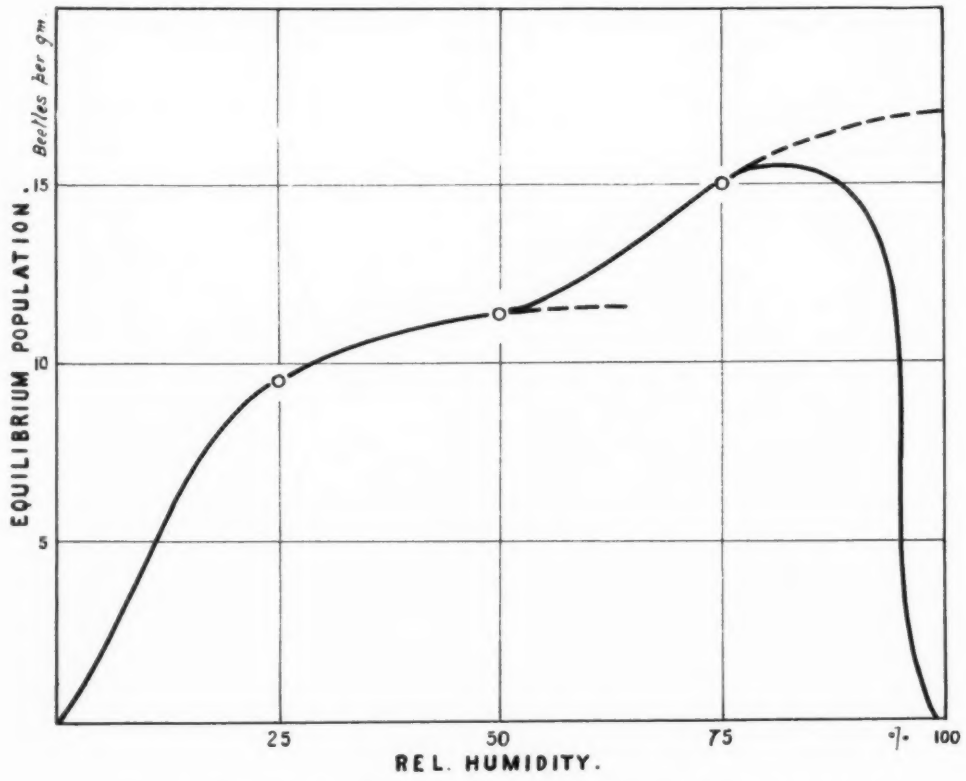

FIG. 4. Showing the relationship between the size of population and atmospheric moisture.

The equilibria of adult populations at different humidities are shown graphically in Fig. 4. A general discussion of the relation between atmospheric moisture and equilibrium populations is given later and indicates the part played by the water content of the food. However, this does not explain why there is a more rapid rise in potential population between 50% and 75% relative humidity than between 25% and 50%. Although at present the full significance of this state of affairs is not understood, it appears probable that an explanation will be found in a fuller understanding of the water-relations of the beetles in regard to the water content of the food. For it is very improbable that the biological water-relations of the insects which involve not only total moisture content, but also the bound and free water equilibrium, all of which are affected by the moisture content of the food and of the atmosphere, should follow the same relationship to atmospheric moisture as does the physical relation between atmospheric moisture and its absorption in flour. In Fig. 4, the portions of the curve between 0 and 25% relative humidity, and between 75% and saturation, must, in the present state of knowledge be considered approximations, but in the light of knowledge of growth phenomena in general are probably quite good approximations.

From a study of Table V and Fig. 3 depicting the growth of populations at different humidities it will be seen that there is also a progressive increase in the *rate* of development of the populations with increase in the relative humidity. For example, in the 75% population (Table III) the newly developed beetles had begun to appear by the forty-fifth day, whereas they were still in the pupal stage in the populations at the lower humidities. At fifty days there were only three new beetles in the population at 25%m., at 50%, 39, and at 75%, 81, making the total adult populations at that time 13, 49, and 91 respectively (Fig. 3).

THE GROWTH OF A POPULATION UNDER CHANGED CONDITIONS OF RELATIVE HUMIDITY

If, as the foregoing results indicate, atmospheric moisture is a factor in the abundance of *Tribolium confusum,* and one the effect of which under constant conditions can be evaluated in terms of the rate of growth and the magnitude of the population attained, it appears probable that a *change* in the humidity would be reflected in the population. In order to test out this hypothesis, a population nearing equilibrium at 25% relative humidity was placed at 75%, the flour used at the time of the change and thereafter being flour at equilibrium with the latter humidity.

The data on the population trend under such conditions are given in Table VII and represented graphically in Fig. 5. The change from 25% to 75% relative humidity took place after the population had been at the lower

humidity for 71 days. From this time onwards the growth of the population was materially changed; a slight effect was shown in a few days, but after 15 days the effect was more pronounced (Fig. 5); instead of continuing in its former trend and reaching an equilibrium in the vicinity of 180 beetles, there was an upward trend which ultimately resulted in a mean population of 309 being reached. This population is of the same order of magnitude as that attained by populations maintained at 75% relative humidity throughout.

TABLE VII. *Change in growth of population after changed environmental humidity. Temperature, 27° C.*

	Days	Eggs	Larvae	Pupae	Adults	Total
25% Relative Humidity.	0	...	..	..	10	10
	11	131	0	0	10	141
	20	218	78	0	10	306
	30	197	189	0	10	396
	40	166	307	0	10	483
	45	...	...	24	10	...
	50	137	355	84	13	589
	55	...	...	102	52	...
	60	132	362	95	110	699
	65	...	...	71	153	...
	71	253	269	50	187	759
75% Relative Humidity.	75	...	...	41	197	...
	80	530	183	55	210	978
	85	...	...	67	218	...
	90	695	58	77	252	1082
	95	...	..	31	279	....
	100	552	66	8	288	914
	110	545	74	1	290	910
	115	...	..	14	289	...
	120	708	54	18	289	1069
	130	781	111	4	294	1190
	140	600	163	0	299	1062

DISCUSSION

It is evident from the foregoing sections that in the case under consideration, atmospheric moisture is a decided factor in the rate of growth and concentration of a population, whether that population be at a constant humidity, or whether it be changed from a low to a high humidity during the course of its development. Experimental evidence on the effect of changing a population from a high to a low relative humidity is at present not available, but it would appear very probable that a reverse of the state of affairs occurring in the change from low to high would occur.

Chapman (1928) in his original work on Tribolium populations found that the main factor in bringing about an equilibrium was the destruction of the immature stages, particularly eggs and pupae, by the feeding stages. This is readily seen in the case of the pupae when counts are being made, partially consumed pupae being very evident. The result of egg consumption can be

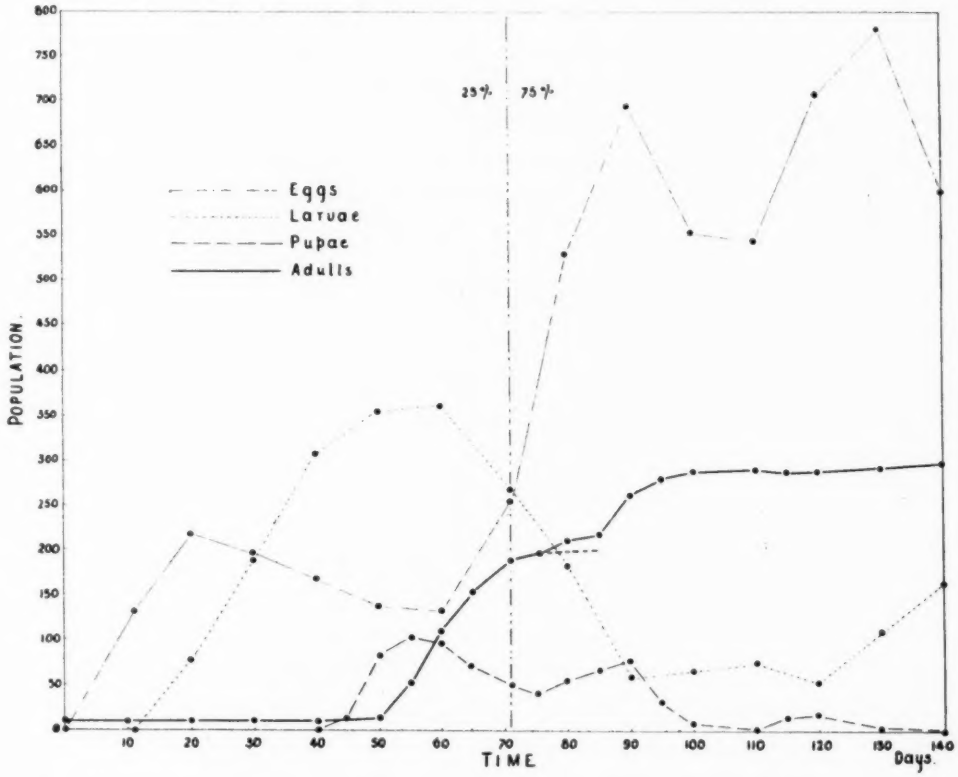

FIG. 5. The change in growth of a population at 25% relative humidity when placed at a relative humidity of 75%. Constant temperature, 27° C.

seen from an examination of any of the tables and their corresponding curves showing the populations when all stages are plotted separately. During the period of equilibrium population, large numbers of eggs are constantly being laid, and large numbers are continually present. Very few of them, however, survive long enough to hatch. In the population at 75% relative humidity, the egg population had been several hundred for two months, and had reached over 700 on the one hundred and thirtieth day (Fig. 2); nevertheless the maximum larval population in this period had been only 72.

Further, considering the population at 75% relative humidity again (Fig. 2 and Table III), it will be seen that the egg population increased until the twentieth day. Hatching which had started before this time was responsible in the main for the subsequent diminution. But from the oviposition records, given in part in a later section (Table XII), for five females of the same age and under the same conditions as those in the populations, it will be seen that the egg production by the tenth day should have been approximately 108. Actually there were 89 present, indicating a reduction of 18%. By the twentieth day 495 eggs should have been laid; actually there were 214 eggs and 94

larvae present. With a hatching of 86.6% at 75% relative humidity (Table X) the 94 larvae would have been derived from 109 eggs. These with the 214 eggs present make a total of 323 eggs instead of the 495; and this represents a reduction of 35% since the beginning. By the thirtieth day the actual progeny surviving indicated a reduction of 46%. The comparison between the theoretical and actual populations to this point is summarized in Table VIII.

TABLE VIII. *Comparison between actual and theoretical populations at 75% relative humidity.*

Days from beginning	Actual Population		Egg Equivalent of larvae	Population in terms of eggs laid	Theoretical Population (eggs laid)	Survival, %	Reduction, %
	Eggs	Larvae					
10	89	0	...	89	108	81	19
20	214	94	109	323	495	65	35
30	186	254	294	480	886	54	46

From these facts and from a consideration of the viability of all stages at particular temperatures and humidities, the theoretical population possible under these conditions may be obtained. Actually the theoretical geometric growth of the population does not take place. If it did the population would increase so rapidly and reach so high a concentration in a very short time that no food would remain and the population would perish. This maximum rate of increase is given by the formula

$$P = ne^{kt};$$

where P is the population at the end of time t; n, the initial population; and k, the rate of increase. But in nature the maximum rate of increase does not continue beyond a short period of time. There is generally some provision whereby the numbers are kept down and a more optimum concentration maintained, so that the food supply does not constitute a limit to the survival of the species. For example Richards (1928) has demonstrated in yeast populations that decrease of food in the medium is not a causal factor in the decrease in the growth rate. When the latter is diminished it is usually due to the decrease of an essential substance rather than to a general decrease of all the nutrient. In the case of Tribolium atmospheric moisture is one of these "essential substances." The mechanism bringing about the decrease will naturally differ in different systems but the principle is the same.

The limitation to over-population may be of a biotic nature, due to predators in the widest sense of the word, to some physical factor of the environment, or to a limit imposed by the species itself. Interesting examples of all types occurring in animals are given by Elton (1927). In the case of microorganisms, chemical factors such as a decrease in "bios" or the increase in the alcohol content of the environment, directly resultant on the population

are of prime importance in regulating the numbers (Clark, 1922). With Tribolium the limiting mechanism is a biotic one produced by the species itself. The insect becomes a predator on its own kind with increasing magnitude as the population increases. This control is brought about largely by the increased chance of immature stages being encountered by the feeding stages as the population grows. But the fact remains that the controlling effect which Tribolium is capable of exerting on itself is only one particular form of the wide principle of limitation against over-population which occurs throughout nature.

Recently the writer while working on the ecology of carrion insects in France, has encountered a case of limitation of population, not only similar in principle to that which operates on Tribolium but also in mechanism. The immature stages of the carrion beetle *Saprinus nitidulus* Payk *(Histeridae)* are subterranean and feed on the puparia and to some extent the larvae of certain flies, *Lucilia sericata* Meign. and species of Sarcophagidae. When the puparia are few, the histerid larvae feed to a greater extent on their own eggs and probably also their own larvae in the soil; the histerid population is thus limited, but the individuals which do remain are at least assured of sufficient food for development. Another example of self-control is that recorded by Salt (1929) for *Lucilia sericata,* and also observed in nature by the writer (1930). Here again the potential reproductive rate is much higher than available food can support; a reduction of population takes place by competition *inter se.* In nature other competitive agencies also contribute, but for the present, the important point is that self-limitation is possible and does occur.

Let us now turn for a moment to a brief consideration of certain aspects of the physiology of Tribolium. Babcock (1912) found that the water content of the larvae was 62.43%, and of the adults 50.38%. The moisture present in the food in which they were living was about 10%. This indicates that Tribolium is capable of maintaining its water content at a level considerably above that of its food, evidently by the utilization of metabolic water, which with many animals is almost entirely excreted.

At a low relative humidity, flour has a small percentage of absorbed water. Moreover, since flour beetles will feed on the immature stages and dead bodies of their kind, it appears that we have an explanation of the reason for different equilibria at different humidities. At higher humidities with more moisture available in the flour it appears that the attack on pupae and eggs is not so severe as at the lower humidities where apparently they serve as a more ready source of moisture than does the flour for the maintenance of the necessary water content of the feeding stages.

A consideration of the results obtained from the population developed originally at 25% and then placed at 75% relative humidity will support this

suggestion. At 71 days (Vide Fig. 5) when the adult population was approaching equilibrium, the pupal population was decreasing. With the addition of more moisture to the flour through the change to a higher humidity, fewer pupae were consumed. This was reflected first in the increase to the rate of adult emergence and this in turn led to an immediate small increase in the adult population up to the eighty-fifth day. It was also reflected in the marked increase in the pupal population after the seventy-fifth day, although the pupal population was also contributing to the increase in the number of adults. This greater survival of individuals pupating after the seventy-first day was ultimately shown in a more pronounced increase of the adult population after the eighty-fifth day. However, almost immediately the effect was reflected in the increased consumption of pupae by the larger adult population, which resulted in a decrease in the number of pupae and the acquirement of a new equilibrium population.

If now we consider the reduction in potential population in the early stages of population growth at 50% and at 75% relative humidities, further striking evidence of the way in which humidity affects the equilibrium population is obtainable.

Table VIII gives the reduction in potential population which occurs during the first 30 days of growth at 75% relative humidity, namely: 19% reduction by the tenth day; 35% by the twentieth day; and 46% by the thirtieth day. From a consideration of the growth of populations at 50% relative humidity (Table IV) and the mean oviposition (Table XII) of a number of beetles equal to the initial concentration in the population and at the same conditions, the reduction in potential population at *50%* relative humidity will be as is shown in Table IX. It is apparent that from the beginning the

TABLE IX. *Comparison of actual and theoretical populations at 50% relative humidity and 27 C.*

Days from beginning	Actual Population		Egg Equivalent of larvae	Population in terms of eggs laid	Theoretical Population (eggs laid)	Survival, %	Reduction, %
	Eggs	Larvae					
10	97	..	..	97	138	70	30
20	187	84	99	286	565	51	49
30	152	216	254	406	988	41	59

population at the higher humidity is not subjected to as great a reduction as is the population at the lower humidity. And as the reduction up to this time has been brought about by consumption of eggs by the feeding stages, the writer's hypothesis that at lower humidities the immature stages are more readily utilized as a source of moisture is supported.

It can then be affirmed that the mechanism by which atmospheric moisture regulates Tribolium populations is an alteration in intensity of the nor-

mal biotic control which the species can exert on itself; or in other words, the effect of the physical factor, humidity, on the insect population is *per medium* of a biotic effect the intensity of which is regulated by the physical effect of atmospheric moisture on the moisture content of the flour.

Ecologically, the demonstration of such a state of affairs is highly interesting and the interdependence of physical and biotic factors in their operation will, in the future, be more and more widely demonstrated. Suggestive evidence that such a state of affairs operates in nature is not uncommon, and more observations like those of Seamans (1926) would give strong support to the idea. This worker found that outbreaks of the pale western cutworm, *Porosagrotis othogonia* Moer., in Alberta could be predicted from the preceding rainfall records, or the number of wet days during the spring. If the number of wet days in May and June is less than 10 an outbreak the following year is probable; while if the number is greater than 15 an outbreak is unlikely. The control by rainfall acts indirectly by means of parasites: with increased rainfall and the resulting wetter soil, the larvae move to the surface and are more readily parasitized. Looked at from another point of view, the biological control is only effective when the physical conditions of rainfall are suitable.

While the explanation given may satisfactorily explain the *mechanism* by which different concentrations of Tribolium may be reached at various humidities, the difference in *rate* of development still requires explanation.

From an analysis of the effects of humidity on the components of a population (p. 286) it will be seen that the stage most affected in rate of development is the larva (Table XI, Fig. 7). Larval life at 25% relative humidity requires a mean of 30.1 days for completion, and at 75% only 22.6 days. The more rapid rate of growth of the populations at higher humidities is thus evidently due to the more rapid development of the larvae. This is no doubt due to the more readily available moisture in the flour. At the low humidities, with less available moisture, the provision by metabolism of sufficient moisture for larval development is a longer process.

GROWTH CYCLES

As mentioned in the introduction, workers in various fields have demonstrated that normal growth may be resolved into successive "growth cycles." Examination of the data obtained when populations are submitted to changed conditions of environmental moisture (Fig. 5) indicates two successive "growth cycles." If populations are submitted to numerous changes, positive and negative, the natural growth curve will no doubt to a large extent mask the individual cycles which have contributed to the final population. Such a state of affairs occurs in nature. Any type of insect which begins reproduction in the spring is subjected to a variety of factors, physical, biotic, and

nutritional, which influence the growth of the population. It would not be surprising then in considering natural populations which are comprised of a variety of positive and negative growth cycles to encounter difficulties not only in discriminating between the various growth cycles but in allotting to each factor its particular value. If the natural population comprise interacting forms with life cycles of different lengths, of which some are annual and some triennial to quinquiennial, the problem will be further complicated. Its solution nevertheless is not beyond means of attack, and the excellent work of King (1929) on field crop insects is sufficient proof, not only that such complex problems are open to attack along population study lines, but that such methods are productive of results of outstanding value. The environment supplied by a piece of carrion in nature, although comparatively simple, is much more complex than are the environments mentioned in the present paper. But already the writer in attempting to understand the natural regulation of carrion-feeding insects has had encouraging indications of the value of the application of ideas gained and the point of view developed from these simple population studies (1930).

AN ANALYSIS OF THE EFFECTS OF HUMIDITY ON THE COMPONENTS OF A POPULATION

The effects of different conditions of atmospheric moisture on the stages which constitute a Tribolium population, were studied from the point of view of viability and rate of development. As with the populations these results were obtained at a constant temperature of 27° C. As far as possible each stage for study was obtained from conditions similar to those under which it was desired to study it, e.g. eggs for study at 25% relative humidity were obtained from a culture at 25%, while those for study in a saturated atmosphere were laid in one which had 75% relative humidity. All eggs were removed from the culture, and those laid during the subsequent twelve hours were used in the study.

VIABILITY

The viability, determined by the percentage of each stage completing development at different humidities is given in Table X and represented graphically in Fig. 6. Eggs are very little affected by changed humidity conditions except at a very high relative humidity when development is prevented by the growth of fungi. At 75% there is a higher survival than at 50% relative humidity. Nevertheless at saturation hatching failed to occur. Viability is highest at the low humidities, the maximum occurring in a dry atmosphere. This is contrary to the opinion expressed by Headlee (1918) with regard to *Bruchus obtectus* Say., another stored product insect. Since when Bruchus eggs were placed on beans in 1% moisture no progeny were obtained, Headlee concluded that the egg stage was the most susceptible to low moisture conditions. Had the eggs been studied separately for hatching, it is possible that a different conclusion may have been reached.

TABLE X. *Survival at different humidities.*

Eggs

Relative Humidity, Percent	Eggs	Percent Hatching
1	300	89.3
25	250	89.2
50	250	85.2
75	300	86.6
99	200	0*

*Heavy fungus growth.

Larvae

Rel. Humidity, Percent	Larvae	No. Pupating	Percent Pupating
25	321	295	91.9
50	940	916	97.4
75	516	508	98.7

Pupae

Rel. Humidity, Percent	Pupae	No. Emerging	Percent Emerging
1	174	174	100
25	156	156	100
50	147	138	93.9
75	138	115	83.3
99	185	54	29.2

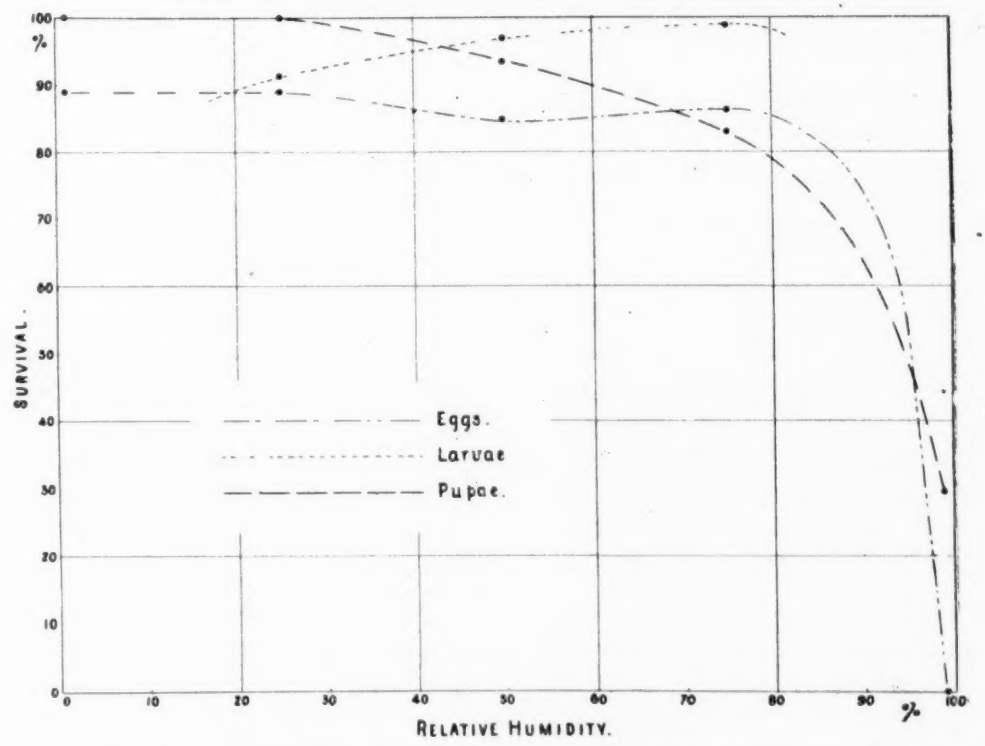

FIG. 6. Graphic representation of the viability of eggs, larvae and pupae of *Tribolium confusum* at different humidities. Temperature, 27° C.

Groups of larvae developed under conditions ranging from 25% to 75% relative humidity, show an increase in percentage survival with increase in humidity (Fig. 6). No special experiments on survival of larvae were made in dry and saturated atmospheres, but an attempt to develop Tribolium in a saturated atmosphere resulted in failure due to the growth of fungus on the flour. It is thus highly probable that survival of larvae reaches a maximum at about 75% and falls to a minimum at saturation. Further, since the percentage of survival decreases from 75% to 25% relative humidity, it also seems probable that another minimum for survival would occur in a dry atmosphere.

Pupae exhibit 100% emergence in dry atmospheric conditions up to 25% relative humidity. Above 25% there is a decrease in the percentage of survival until a minimum viability of 29.2% is reached at saturation.

RATE OF DEVELOPMENT

(a) *Eggs.* By recording the number of eggs hatching each twelve hours records on the rate of development were obtained from the same batches as were used for studying viability. There was little variation on account of change in atmospheric moisture. The slight difference observed indicates a maximum rate of development at 50% relative humidity, or a stage duration of 12.2 half days. The minimum rate occurred in 1% relative humidity, the duration of the egg stage under these conditions being 13.1 days. No emergence was obtained in saturated air, owing to the development of fungus on the eggs. The data for each humidity are given in Table XI and the

TABLE XI. *Duration of stages at different humidities.*

Eggs

Relative Humidity, Percent	Eggs	Mean Time; half days
1	300	13.1
25	250	12.3
50	250	12.2
75	300	12.7
99	200	(No emergence owing to fungus growth).

Larvae

Relative Humidity, Percent	Larvae	Mean Time; days
25	173	30 1
50	366	25.5
75	507	22.6
99	...	....

Pupae

Relative Humidity, Percent	Pupae	Mean Time: half days
1	74	15.9
25	156	16.2
50	141	16.3
75	115	16.2
99	54	15.4

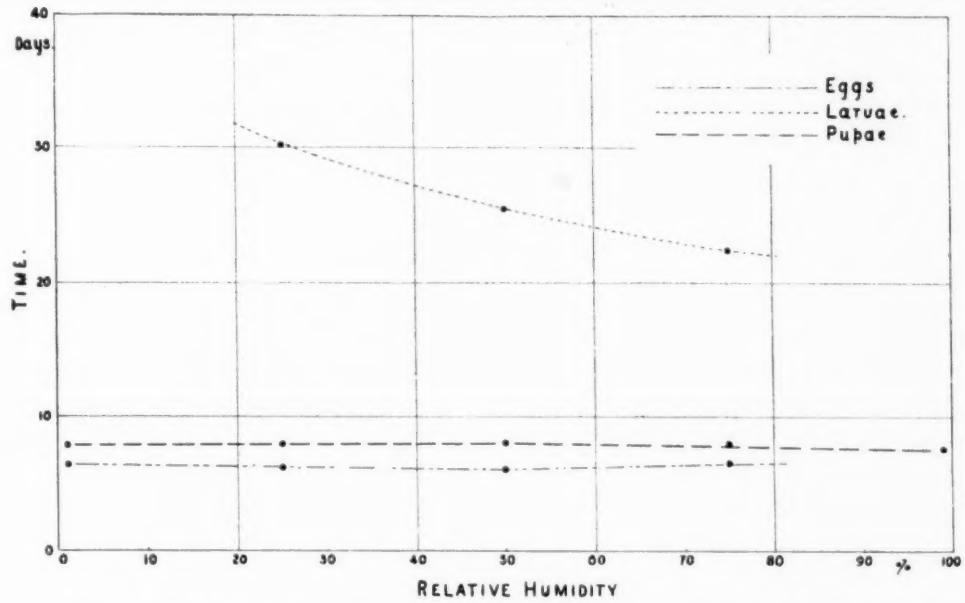

FIG. 7. Duration of the stages of Tribolium at different relative humidities. Temperature, 27° C.

duration of the stages represented together with that of larvae and pupae in Fig. 7. The mean duration of each stage is calculated as:

$$\bar{x} = \frac{\Sigma n_1 r_1}{n}$$

where n_1 = the number completing the stage on each half day, r_1 = the number of half days from the beginning of the stage to the particular half day, n = the total number completing the stage.

Apart from the absence of hatching in a saturated atmosphere, it is evident that the eggs of *Tribolium confusum* are little affected by change in atmospheric moisture. Many organisms, particularly those living normally in moist situations exhibit the reverse state of affairs. In such cases the egg stage is able to withstand drying and is prolonged almost indefinitely until the return of moisture brings it to an end by causing hatching. The "springtail," *Smynthurus viridis* Linn., a pest of Lucerne and clovers in South Australia is such a case (Holdaway, 1927). Under dry conditions the egg stage

has been prolonged to over 270 days, and was terminated by hatching only after addition of moisture.

(b) *Larvae.* Larvae have been developed in three humidities in flour at equilibrium with the respective moisture conditions. Development is more rapid in the higher humidities, the mean time for larval life being 22.6 days at 75% relative humidity, 25.5 days at 50%, and 30.1 days at 25%. As mentioned previously this is no doubt correlated with the fact that the moisture for life and growth is largely obtained by utilization of metabolic water. At the higher humidities, at which the flour has more adsorbed moisture, the growing larvae have more free water available in the food. This evidently results in the drain on metabolism for water being lessened and in larval development being completed in a shorter time. The mean times for development as given in Table XI are calculated by the formula mentioned in the previous section.

The sexes of *Tribolium confusum* are readily determined at pupation; it was thus possible to know the number of each sex pupating each day. The graphic representation of the pupation of larvae developed at different humidities is seen in Figs. 8, 9, 10 and 11, in the first three of which the pupation of sexes is given in broken lines, while the total population is represented by a solid line. Each reading represents the percentage of the total larvae used which pupated on the particular day; the curve represented by the solid line is thus the sum of the curves represented by the broken lines.

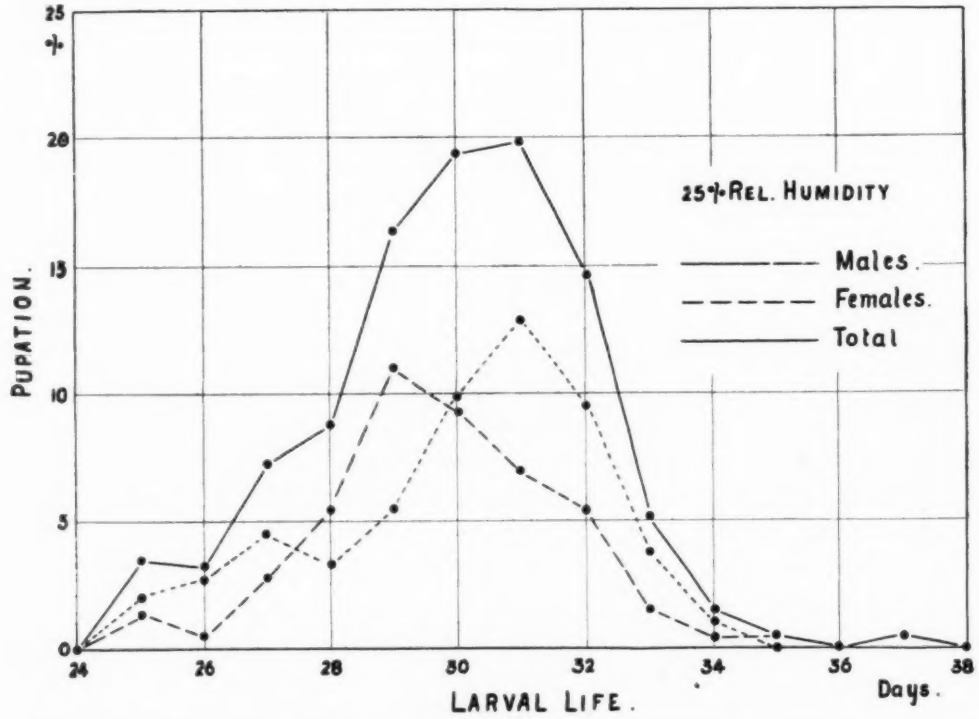

FIG. 8. Graphic representation of the larval life and pupation of larvae of *Tribolium confusum* developed at 25% relative humidity. Temperature, 27° C.

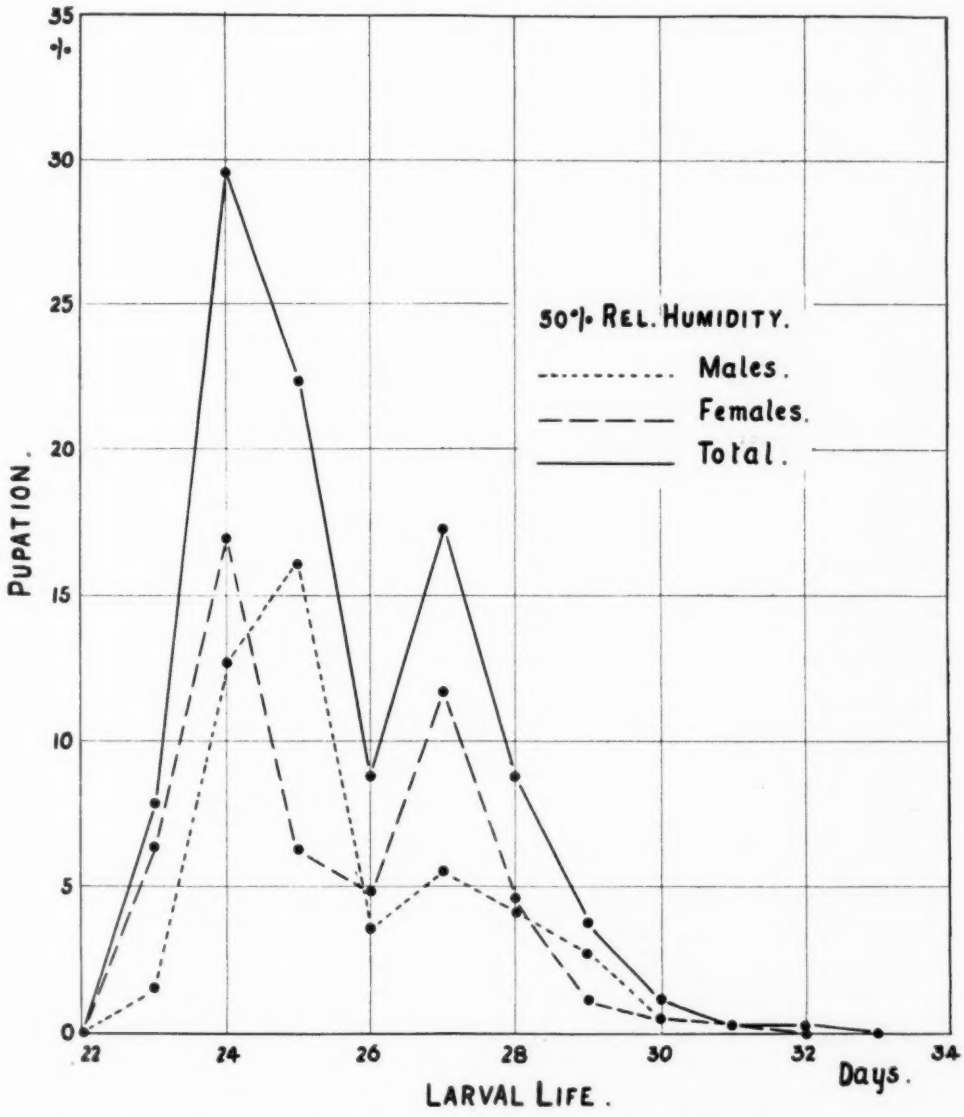

FIG. 9. Larval life and pupation of larvae developed at 50% relative humidity. Temperature, 27° C.

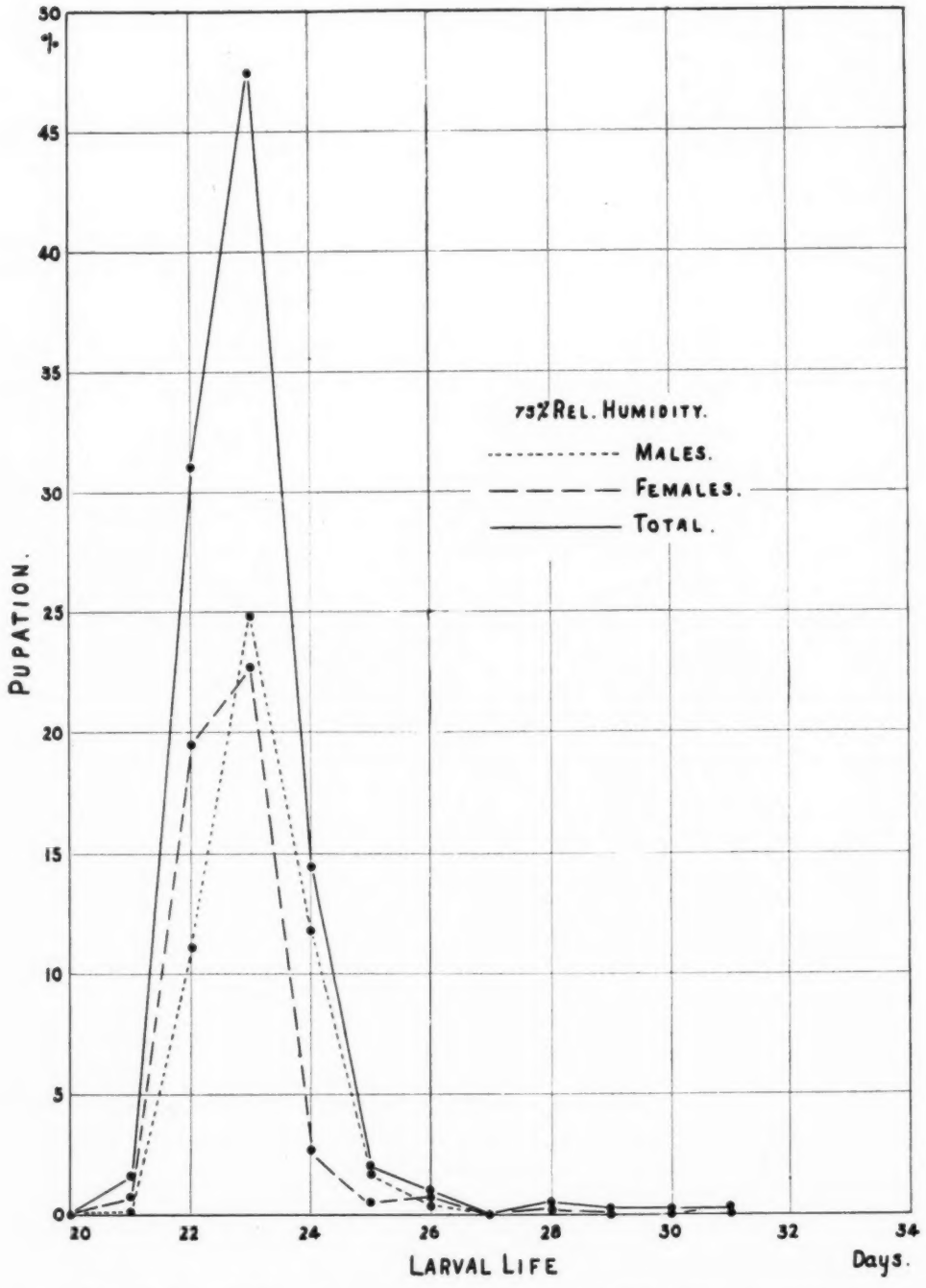

FIG. 10. Larval life and pupation of Tribolium at 75% relative humidity. Temperature, 27° C.

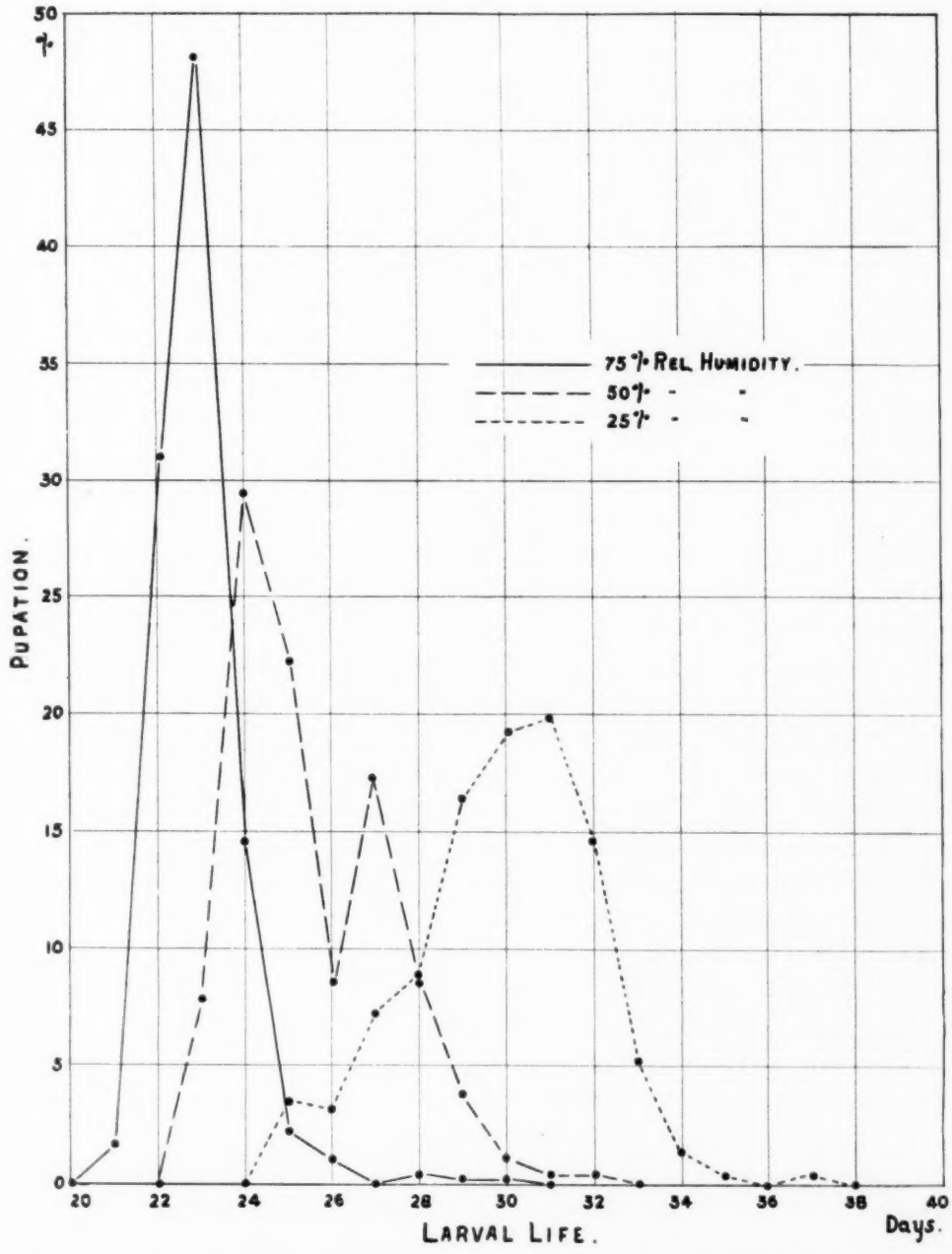

FIG. 11. The larval life and pupation of *Tribolium confusum* at 25%, 50% and 75% relative humidities. Temperature, 27° C.

One thing which stands out from these curves, especially from the one showing larval life and pupation at 50% relative humidity, is their bimodal condition. The curves are constructed from results obtained from several batches at each humidity, and when the data for each batch is plotted separately the bimodal condition is seen in each case.

It would be unwise to draw conclusions on these data alone, but as there is here foreshadowed a suggestion of quantitative sexuality which has been studied at greater length than is here reported, brief attention is drawn to the point. The work, which has indicated that individuals considered to be one or other of the two sexes may be, in part at least, individuals transformed from the opposite sex, has already been considered briefly (Holdaway, 1930) and will be dealt with in greater detail at a future date.

(c) *Pupae.* A study of the effect of different humidities on the rate of development of the pupae has indicated little change due to various conditions. Contrary to what was found with the eggs there is an indication of a minimum rate of development at 50% relative humidity, 16.3 half days, with an increase in rate to 15.9 half days at 1% and 15.4 half days at saturation. The data are given in detail in Table XI and Fig. 7.

OVIPOSITION

Oviposition records at different humidities have been obtained as follows: Beetles just emerged and still pale in color were always used; five pairs were taken for each humidity, and each pair was confined in a separate wide-necked glass tube open to the air. As with the population experiments, only whole wheat flour at equilibrium with the particular atmospheric humidity was used, and this was renewed every ten days. Initially a small amount of flour, 3 grams per pair, was placed in each container, in order that mating might be facilitated. After five days the amount was made up to 10 grams per pair, to reduce the chance of adults encountering eggs and consuming them. Oviposition records obtained prior to the beginning of the main experiment had suggested that the agitation caused by sieving the beetles as often as every day might in time adversely affect the egg production. The method therefore adopted to secure daily records was as follows: The contents of each container were poured out on to a bolting cloth sieve; as the pair of beetles freed themselves from the flour they were removed to an empty container with a moistened camel-hair brush. The flour was then sieved to remove the eggs, and the beetles replaced in it.

Oviposition records were obtained at the three humidities at which populations were developed, namely, 25%, 50%, and 75% relative humidities respectively. Laying began first at 50%, with one egg on the sixth day and 24 from the five pair on the seventh day. It began a little later at 75% relative humidity, 0 eggs on the sixth day and 9 on the seventh. At 25%, 0 eggs were recorded on the sixth day and only 1 on the seventh day. The accumulated totals showing the initiation of oviposition and its continuance for the first 16 days of life at the three humidities are given in Table XII. It will be seen that in addition to the oviposition beginning at 50%, next at 75%, and later at 25% relative humidity, the magnitude of oviposition at these conditions is

TABLE XII. *Oviposition during the first sixteen days of life at different humidities. Five pair of beetles at each condition.*

Days since emergence	6	7	8	9	10	11	12	13	14	15	16
25% R. Hum.	0	1	13	41	73	103	135	171	198	235	262
50% R. Hum.	1	25	59	96	138	173	215	253	293	331	382
75% R. Hum.	0	9	36	71	108	159	196	231	266	301	333

in the same order. The mean egg production per female per day of life was 25% Relative Humidity, 3.27; 50%, 4.77; and 75%, 4.16. The records of individual females show that by the ninth day, oviposition had reached a rate characteristic of the normal laying period of all the humidities studied. The data obtained from the tenth day onward thus serve for calculation of the mean oviposition rate for the normal laying period.

Laying records at 25% relative humidity are available for only 16 days of life, which allows of calculation over a normal laying period of 7 days or 35 female days. At 50% and 75% relative humidity, however, the records are available for a longer period, 42 days of life, thus providing oviposition records over a normal laying period of 33 days. The mean oviposition at 25% relative humidity is thus calculated from 35 female days, while for the other conditions it is calculated from periods of 70 and 165 female days in addition. The gross egg production and mean oviposition are given in Tables XIII and XIV.

TABLE XIII. *Gross egg production by five females at different humidities during the normal laying period.*

Relative Humidity, Percent	7 day period. 10–16 day	14 day period. 10–23 day	33 day period. 10–42 day
25	221	...	...
50	286	578	1335
75	261	523	1228

TABLE XIV. *Mean egg production per female day at different humidities.*

Rel. Humidity, Percent	35 Female Days	70 Female Days	165 Female Days
25	6.3	...	...
50	8.2	8.3	8.1
75	7.5	7.5	7.4

The mean oviposition up to an age of 42 days is thus seen to vary little according to the period over which the calculation is made. The data suggest a slightly higher oviposition rate at 50% relative humidity than at other conditions. There is however quite a significant variation in egg production in

different females compared with the difference in mean oviposition at different conditions, as will be seen in Table XV.

TABLE XV. *Mean oviposition records at different humidities.*

Rel. Humidity, Percent	Number of Female Days	Mean Daily Oviposition	Standard Deviation	Standard Error
25	35	6.3	±2.27	± .38
50	70	8.3	±2.78	± .33
75	70	7.5	±2.14	± .25

By considering the standard error of the differences as equal to $\sqrt{\sigma_1^2 + \sigma_2^2}$; where σ_1 and σ_2 are the standard deviations of any two means, it is found that the difference between the mean oviposition at the different humidities might fall within the range of normal variation. In other words the variation in oviposition rates of individual females is capable of masking any difference, due to different humidities, which may exist. Only when more is understood of the metabolic differences distinguishing individual females, and pure line strains have been bred will it be possible to study the matter to complete satisfaction. Meanwhile although there might be slight differences in oviposition rates according to humidity, particularly as the difference suggested is similar to that noted at the beginning of oviposition (*i.e.* an optimum at 50%) the point remains unproven.

It is not known how long individual beetles may live. However of those used for oviposition records at 50% and 75% relative humidities, both males and females of every pair were still alive 63 days after emergence. Up to 42 days there was no appreciable sign of decrease in oviposition. The females originally present in each population were thus still alive and reproducing at a time when the point of inflection of the growth curve for the adult population which was their progeny had been passed and the acceleration of the growth rate had become negative.

THE EFFECT OF HUMIDITY ON TRIBOLIUM FROM THE POINT OF VIEW OF ITS EFFECT ON A POPULATION

A consideration of the effects of humidity on the components of a population as given in the foregoing sections indicates a diversity of effect both as regards viability and duration of the stages. For example, viability of the eggs and pupae is at a maximum at low humidities (Fig. 6), while for larvae it is at a minimum. As regards the duration of the various stages, there is little effect apparent on eggs and pupae. What effect is shown indicates that there occurs near 50% relative humidity a maximum period, or a minimum rate of development for pupae, while at the same conditions there occurs for eggs a *minimum* period or a *maximum* rate of development. The larval stage

is the one in which duration is most affected by atmospheric moisture. It increases with decrease in humidity.

If one were to consider only the hatching of eggs and the emergence of pupae, one might conclude that lower humidities were more ideal for Tribolium than are the higher, since the maximum of hatching and the maximum of adult emergence takes place under dry conditions. The oviposition records although inconclusive suggest a lower oviposition rate at 75% than at 50% relative humidity, and the possibility that the higher moisture condition was less suitable to the development of large numbers than was the lower.

If now the results of the population studies are considered with these facts in mind, it is apparent that any conclusion regarding optimum conditions for development of the species in numbers, based on the physiological effect of the environment on any particular stage or function, or even on more than one, does not necessarily give an indication of its effect on the population; for the physiological effect on such important phenomena as oviposition, hatching and emergence of adults leads to *the opposite conclusion to what is actually the case*. As regards development of a population, 75% relative humidity is more ideal than 50%, and 50% more than 25% for at the higher humidities populations of greater magnitude are possible than at the lower humidities.

In nature the factors which affect an insect's abundance are numerous and inter-related. Regardless, initially, of how they act, the ultimate population is capable of providing the algebraic sum of all these effects. From such results the way is opened for determining the "pluses" and the "minuses" with their relative magnitude, and the factor which by its alteration is most significant in affecting the ultimate population.

A large proportion of economic problems in Entomology owe their importance to the number of insects present—the population. In such problems the study of any particular aspect of an insect's physiology may readily indicate the most significant factor in its environment contributing to its abnormal numbers. On the other hand it may not; and as in the present case the study of important physiological phenomena may lead to the opposite conclusion from that actually indicating the state of affairs. It would appear then that here is a concept, the greater realization of which should advance one of the most important phases of investigations in economic problems, the understanding of the "why" and the "wherefore" of insect numbers.

CONCLUSIONS

The conclusions which have been drawn from the foregoing are as follows:

1. At constant temperature conditions a given mass of flour is capable of maintaining populations of *Tribolium confusum* which differ in magnitude according to the conditions of atmospheric moisture.

2. At the moisture conditions under which studies were made (25%, 50%, and 75% relative humidity) there is an increase in the magnitude of

the population possible as the relative humidity increases from 25% to 75%. As conditions approach saturation, the magnitude falls to zero, population growth in such conditions being impossible owing to the development of fungus.

3. Since, as Chapman (1928) has shown, populations at equilibrium can be expressed in terms of the population per unit environment (beetles per gram) the effect of atmospheric moisture on Tribolium may be evaluated in terms of its effect on the population per unit environment.

4. The populations per unit environment, 9.5 per gm. at 25%, 11.4 per gm. at 50%, and 15 per gm. at 75%, show an increase in population with increase in humidity of 20% as the relative humidity increases from 25% to 50% and an increase of 58% as the humidity rises from 25% to 75%.

5. The rate of growth of a population is also a function of the atmospheric moisture, the rate increasing with rise in humidity.

6. When the atmospheric moisture is increased, populations developing under dry conditions and tending to reach an equilibrium characteristic of those conditions, change their rate of growth and eventually reach a population equilibrium characteristic of the higher moisture condition. The growth of populations submitted to such changes can be resolved into successive growth cycles.

7. Different conditions of atmospheric moisture affect the various stages of the insect in rate of development and in viability.

8. A relative humidity which is optimum for rate of development of a stage may be the opposite for viability and *vice versa*, while an optimum humidity for one stage may be the reverse for another stage.

9. Some of these differences in physiological effects of humidity on the insect become of little importance when the effect of humidity is considered from the point of view of its effect on a population.

10. The rate of growth of Tribolium is affected to the greatest extent by the effect of humidity on the rate of development of the larvae.

11. The equilibrium population and also the population growth at different humidities is primarily a function of the amount of adsorbed water in the food.

12. The mechanism by which different population equilibria characteristic of different humidities are brought about is *per medium* of the biological control which the insect is capable of exerting on itself. The magnitude of this biological control is dependent on the atmospheric moisture which affects the moisture content of the flour.

13. The self-control exerted by Tribolium is only one phase of the general principle of control which operates in Nature and prevents over-population. There is thus evident a relation between a physical factor (humidity) and the activity of a biological control, actually *an interdependence of biological control and physical conditions.*

14. It is not possible to conclude from a study of the physiological effects of atmospheric moisture on the insect what the effects of humidity on the insect population will be; the reverse conclusion from what is actually the case may quite easily be reached.

15. The significance of these results to economic problems lies in the fact that they stress the importance of endeavoring to understand the effect of a factor or factors, physical or biological, on an insect, in terms of the effect on the insect's population.

ACKNOWLEDGMENTS

The work was carried out under the direction of Dr. R. N. Chapman. It is a pleasure to acknowledge my indebtedness and express my thanks to him for his keen personal interest, assistance and encouragement. I am also indebted to Dr. R. A. Gortner for his stimulating interest and to Dr. William Robinson for his ready assistance in many aspects of the work. The investigations here recorded were carried out in the Division of Entomology, University of Minnesota, in 1928 during the tenure of a research fellowship under the "Science and Industry Endowment Act," Commonwealth of Australia. To the Trustees of the Endowment Fund I gratefully acknowledge my indebtedness.

SUMMARY

The effect of atmospheric moisture on an insect, *Tribolium confusum* Duval, has been studied from the point of view of its effect on a population in a unit environment. The effect of humidity on the physiology of the stages which constitute the population has also been studied and a comparison made of the evidence yielded from both lines of inquiry. As a result the importance of population studies to problems in economic entomology has been stressed and the opinion expressed that physiological investigations on an economic insect should be carried out collateral to general population studies rather than as investigations confined to the purely physiological sphere.

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THE EFFECT OF SEASONAL VARIABILITY UPON ANIMAL SPECIES IN TOTAL POPULATIONS IN A DECIDUOUS FOREST SUCCESSION[1]

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[1] Contributions from the Zoölogical Laboratory of the University of Illinois, No. 423.

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INTRODUCTION

The discovery of the important animal species of biotic communities is recognized as a fundamental need in the field of modern ecology. In order to discover these important species it is essential to have a knowledge of the dynamic relations existing within the communities, as shown by the responses of the populations to the constantly changing biotic and climatic conditions of the environment. The manifestation of these responses is evident in the fluctuations of population abundance from season to season and year to year.

The determination of the intricate biotic relations of the community necessitates prolonged study of the interrelations of the individuals and species themselves; while a study of the seasonal and annual variability in the populations and of coincident climatic conditions, should furnish a correct interpretation of the effect of a given set of weather conditions upon the community. The years 1925 and 1926 were used in an effort to find out as much as possible concerning these relations as they exist in the biotic communities of a deciduous forest succession in Champaign and Vermillion counties, Illinois. An expression of the general results of these observations was given in a previous paper (Smith, '28). Since then a more detailed analysis of the data has contributed some new and interesting findings to the investigation.

The writer wishes to express her appreciation for the advice and assistance of Dr. V. E. Shelford in this work; and to the specialists who made specimen determinations. A list of the latter has been included in a previous paper (Davidson, '30).

THE BIOTIC SERE

In making a choice of territory for the study of a woodland sere, the lower coal strip mine lands of Vermilion County, Illinois, were decided upon as a suitable region for observations of the early stages, since it was possible to select areas ranging from those recently mined-over and bare to those which have been in the process of re-vegetation for twenty-five years. Besides the stages of the succession developing normally to upland forest, the presence of the Salt Fork River makes possible a second type in which development is towards bottomland forest. Stages in both seres were selected for study. The climax units were Brownfield Woods and University Woods which are located a few miles northeast of the University of Illinois. The presocies[1] (Stages I-IV) were selected on the basis of the amount and kind of vegetation present, and the length of time since denudation, and the presocieties (Stage V) because of their comparatively undisturbed, virgin condition.

[1] The term presocies is a bioecological term referring to the smaller non-dominant organisms of a biotic community. Here it is the equivalent of "animal associes," while presocietv is the equivalent of animal association. The work was carried on relative to biotic communities in which the larger and more influent animals have been either exterminated or reduced in numbers.

The pioneer or *Tarsotomus-Dictyna* Presocies (Stage I) lies within a recently stripped area and is without a vegetational cover most of the year, since only a few annuals appear late in the season and soon die down. The clover-covered ridges or *Lygus-Formica-Chaetocnema* Presocies (Stage II) have a heavy growth of *Melilotus alba* Desr. during estival and serotinal socies, and are covered with the dried stalks of the clover during the remainder of the year. Mention has been made of the fact that two successions occur in the lower striplands. The forest edge or *Helodrilus-Euscelis* Presocies (Stage III) and the flood plain forest or *Theridion* Presocies (Stage IV), located along the Salt Fork of the Vermilion River and subjected to frequent floodings during times of heavy rains and high water, belong to the bottomland forest succession. The *Peromyscus-Erythroneura-Dicyphus-Carychium* Presociety (Stage V) belongs to the maple-red oak climax forest of Central Illinois. A more detailed description of these habitats, with reference to additional literature, is given in a previous paper (Smith, '28).

Field observations were begun in June, 1925, and continued until September, 1926, thus making possible a comparison of the occurrence of animal species during the active, growing seasons of consecutive years. The invertebrate population was sampled by the use of a sweepnet in shrub and herb strata (50 sweeps with an insect net of 30 cm. diameter) and by examination of the ground surface and upper 10 cm. of soil. The field worker in modern ecology is retarded in securing satisfactory results because of inadequate collecting methods. No single method has been devised which affords a complete sampling of the population, and the observer is dependent upon a combination of methods (sweepnet, trapping, cruising, etc.). Although interesting and valuable findings have been made by the use of these methods, they are, however, insufficient and it is hoped that increased interest in this field will bring about the development of new and more adequate methods. The present discussion is limited to the invertebrate populations of the seral communities, since they are more adequately sampled by the present methods and show a quicker response to changing climatic conditions than do the vertebrate populations.

WEATHER VARIABILITY DURING THE YEARS OF 1925 AND 1926

Continuous quantitative field observations may inform the worker as to the common and abundant occurrence of the animal species in the community from season to season and year to year. However, such findings are not sufficient in themselves for an interpretation of the effect of seasonal variability upon the community. They should be accompanied by records of the coincident weather conditions in order to determine the responses of the populations to the effects of varying seasonal conditions.

The climatic factors considered in 1925 and 1926 are temperature, humidity, and rainfall. Continuous records of soil and air temperature and relative humidity were kept in University Woods (Stage V) climax throughout the period of observation, and in the clover-covered ridges of the striplands (Stage II, early seral stage) from March 22 to September 6, 1926. For graphic presentation of these conditions, and of rainfall[2] see Figs. 1 and 2.

The data resulting from the measurement of temperature and relative humidity are reported as weekly and seasonal means (weekly and seasonal averages of the two-hourly readings), and as weekly and seasonal mean ranges (differences between the averages of the daily maxima and of the daily minima for the week and for the season). The seasonal means and the seasonal mean ranges are used for the purpose of eliminating minor daily and weekly variability.

In general it may be said that 1926 was a much wetter summer than 1925. The rainfall averaged from 3 to 6 inches more during the estival and the serotinal seasons. In the climax community the relative humidity reached a 15 per cent higher mean during the serotinal season, with a correspondingly lower mean range. Mean air and soil temperatures were a little less in the estival season of 1926 and slightly higher in the serotinal season, while mean range of air temperature was considerably lower and mean range of soil temperature slightly higher (Fig. 1). Unfortunately measurements of weather conditions could not be made in the subclimax stages during 1925. However, Fig. 2 illustrates the relative instability of a subclimax stage as compared with the climax stage in regard to temperature and humidity conditions for the year 1926. In all cases it is evident that the mean range of soil and air temperatures is greater in the seral stage. In general the same conditions of greater variability in Stage II holds good for range of relative humidity. This tendency of the climax forest to temper the weather in the direction of less extremes is illustrated likewise in the means. Although both the climax and seral stages, where weather instruments were maintained, were subjected to the same climatic conditions the forest actually maintained a more humid and cooler climate as measured by the averages of the two-hourly readings.

THE FLUCTUATIONS IN ABUNDANCE OF ANIMAL SPECIES DURING CONSECUTIVE YEARS

The response of individuals of a biotic community to fluctuations in weather conditions may be interpreted in terms of the changing character of the animal population from season to season and year to year. An illustration of the latter may be found in Figs. 3 and 4 for the invertebrate populations of climax and seral communities of a deciduous forest succession during the active growing seasons of 1925 and 1926. The seasonal mean population (average of weekly collections) was used as the basis of comparison. This

[2] From Climatological Data, vols. 30 and 31, U. S. Dept. of Agriculture, Weather Bureau.

basis was used for the purpose of eliminating the effect of minor daily and weekly variability in weather conditions and at the same time for the purpose of emphasizing seasonal and yearly trends.

An inspection of Figs. 3 and 4 reveals three fundamental facts. The first of these facts is that a large number of species reach their maximum abundance in one of the two years. For example it is found that 17 species of the climax forest attain maximum abundance in 1925 as contrasted with 9 species in 1926 (Fig. 3), whereas the subclimax stages show 7 species most abundant in 1925 as compared with 21 species in 1926 (Fig. 4). A detailed analysis of these examples is found in the following summary which gives the species name and the year of maximum abundance. The numbers locate the species in the figures.

Species attaining maximum abundance in 1925:

Climax stage—*Enchytraeidae* (1), *Pokabius bilabiatus* (Wood) (5), *Aphaenogaster fulva* Roger (6), *Mangora gibberosa* Htz (7), *Lasius niger americanus* Emery (8), *Oedothorax flaveolus* Banks (9), *Carychium exiguum* (Say) (10), *Lycosa* sp. (12), *Octolasium lacteum* (O) (13), *Formica* sp. (15), *Epuraea rufa* (Say) (16), *Leptothorax curvispinosus* Mayr. (18), *Erythroneura obliqua* Say (26), *Dictyna* sp. (27), *Xysticus* sp. (29), *Cicurina arcuata Keys* (31), and *Cantharis excavatus* Lec. (32) (Fig. 3).

Subclimax stage—*Acyrthosiphon pisi* (Kalt) (8), *Triphleps insidiosus* Say (10), *Phymata erosa* L. (11), *Diplocephalus erigonoides* Em. (12), *Formica fusca argentata* Whlr. (13), *Chaetocnema confinis* Cr. (14), *Oedothorax flaveolus* Bks. (24) (Fig. 4).

Species attaining maximum abundance in 1926:

Climax stage—*Tomocerus flavescens americana* Schött (2), *Parasitus* sp. (3), *Dicyphus gracilentus* Parsh (11), *Pseudogriphoneura crevecoeuri* Coq. (14), *Agroeca* sp. (17), *Sapromyzosoma philadelphica* Macq. (19), *Phrurolithus palustris* Bks. (22), *Hahnia agilis* Keys (23), *Bathyphantes zebra* Em. (30) (Fig. 3).

Subclimax stages—*Hypnoides pectoralis* (Say) (1), *Tarsotomus spinatus* Bks. (2), *Psylliodes punctulata* Melsh (3), *Aphaenogaster fulva* Roger (4), *Anthicus sturmi* Laf. (5), *Systena taeniata* var. *blanda* Melsh (6), *Dictyna bostoniensis* Em. (7), *Melanoplus differentialis* (Thom.) (9), *Euscelis comma* V. D. (15), *Chloropisca glabra* Mg. (16), *Camptoprosopella vulgaris* Fitch (17), *Melanoplus femur-rubrum* DeG. (18), *Scolops sulcipes* Say (19), *Erythraeus brevitarsus* Ewing (20), *Botanobia salina* Curr. (21), *Anthomyza variegata* Lw. (22), *Camptoprosopella vulgaris* Fitch (23), *Cicadellidae* spp. (25), *Theridion frondeum* Htz. (26), *Aedes vexans* Meigen (27), *Pelastoneurus vagans* Lw. (28) (Fig. 4).

The second of these fundamental facts is that prominent invertebrate species of a given community may reach their greatest abundance during dif-

ferent seasons of consecutive years, *i.e.* a species belonging to the estival season of 1925 may be retarded to the serotinal season of 1926 or species of the serotinal society may be advanced into the estival season. For example, the following species of the climax forest showed maximum abundance during the estival season of 1925 but were retarded to the serotinal season of 1926 (Fig. 3): *Enchytraeidae* (1), *Tomocerus flavescens americana* Schött (2), *Lasius niger americanus* Emery (8), *Carychium exiguum* (Say) (10), *Lycosa* sp. (12), *Epuraea rufa* (Say) (16), and *Xysticus* sp. (29). The following species of the seral stages showed a similar reaction (Fig. 4): *Aphaenogaster fulva* Roger (4), *Dictyna bostoniensis* Em. (7) *Phymata erosa* L. (11), and *Scolops sulcipes* Say (19). In contrast to this retardation reaction, the following species, which reached their maximum abundance in 1925 during the serotinal season, were accelerated to the estival season of 1926 (Fig. 4): *Tarsotomus spinatus* Bks. (2), *Anthicus sturmi* Laf. (5), *Systena taeniata* var. *blanda* Melsh (6), *Melanoplus differentialis* (Thom.) (9), *Chloropisca glabra* Mg. (16), *Camptoprosopella vulgaris* Fitch (17), *Aedes vexans* Meigen (27).

The third of these fundamental facts is that species abundant in one year may be inconspicuous or entirely absent from the collections of the other year. For example, *Phytonomus nigrirostris* Fab. (20), *Ptillodactyla serricollis* Say (24), and *Crematogaster lineolata* Say (25), occurred in 1925 but were absent from the collections of 1926; whereas *Onychiurus subtenuis* Folsom (4), *Isotoma* sp. (21), and *Microneta* sp. (28) were taken only in 1926 (Fig. 3).

A summary of the analysis of the animal populations of the different communities of a deciduous forest succession during 1925 and 1926 shows that the seasonal and perennial predominants of these communities respond to variability in weather conditions. These responses are evidenced in the fluctuating abundance of the individuals and species during favorable and unfavorable years, in the seasonal acceleration or retardation in the development of species, and by the presence or absence of certain species seasonally or annually. The weather of the climax forest during the summer of 1925 was drier and more variable than during the following summer, and is the time when the largest number of species showed greater abundance. Contrasted with this, however, is the fact that more species of the preclimax stages attained a higher abundance in 1926. Unfortunately, it is impossible to compare weather records for the two years in the subclimax stages, but it is evident that weather conditions operate upon climax and subclimax communities to produce different results. It has been shown that during the same year the climax forest tempers the weather conditions to such an extent that the community is actually subjected to a cooler, more humid and less variable climate than are the preclimax communities. If weather records were

available, it is probable that they would show the factors which have produced the different results in climax and preclimax communities. The analysis of these data suggests that one of the characteristics of a climax community is the presence of a large number of species, many of which become prominent only in the more favorable years. This is the answer to several of the difficulties expressed by Blake ('31).

The consistently high relative abundance of spiders, both as perennial and seasonal predominants, makes them an interesting form for further seasonal comparisons in the climax forest (Fig. 5). A comparison of the serotinal portions of 1925 and 1926 illustrates again the relationship previously noted in Fig. 3, *i.e.* the great qualitative variability in the climax societies. The important seasonal forms in 1925, *Oedothorax flaveolus* Bks., *Mangora gibberosa* Htz., *Hahnia agilis* Keys, and a smaller number of *Ceraticelus* sp., show a much changed relationship in 1926. *Mangora gibberosa* Htz. is still important; *Oedothorax flaveolus* Bks., the most abundant spider in 1925, has disappeared entirely from the numerically abundant species, as has also *Ceraticelus* sp.; while a new species, *Agelena naevia* Walck, becomes abundant in the collections. The portion of the graph which gives the picture of the spider population during the time of year when it is most varied strikingly illustrates the qualitative differences between seasons, which this study seems to indicate are *typical* of a *climax community*. It is interesting to note that the frequencies of abundance, both of the seasonal and perennial species, tend to increase with the introduction of the seasons and reach their maximum (modes of abundance) sometimes during the seasonal period. This is in accordance with the conclusion reached by Shackleford ('29) with reference to the correspondence of insect life histories and climatic cycles in prairie communities. The further conclusion might be suggested that the evolution of this adjustment of insect life histories to the climatic cycles may be due to the stimulating influences of the variable climatic conditions coincident with the introduction of the seasons.

RELATIONS OF ANIMAL GROUPS WITHIN THE BIOTIC COMMUNITIES

Any attempt to determine the biotic significance of animals within a community must measure their abundance in terms of the total population of the community. It is apparent that 60 individuals of a species present in the pioneer presocies, having an average population of 268 individuals per square meter (Stage I), will exert a much greater influence upon the community than will the same number of individuals of an equivalent species in the presociety, where the average population per square meter is 2,445 individuals. Figures 6 to 11 give the abundance of six conspicuous groups of animals, analyzed in terms of their percentage relationship to the total population of the same seral stage and the same date. For example, the total population on June 21, in

Stage IV, is 1,134 individuals per square meter, while the total number of Diptera for that date is 191 individuals per square meter; which gives 16.8 per cent Diptera. Six groups of animals prominent throughout the sere have been graphed for prevernal, vernal, estival, and serotinal socies and societies of 1926. Autumnal and hiemal socies and societies of 1925 also are included in the discussion.

Both Fig. 7 and Table 1 show that beetles make up a high percentage of the populations of the seral stages. Since no graphic analysis, similar to that included for spiders in Fig. 5 is included for beetles, a short discussion of the specific make-up of the various peaks and depressions shown in Fig. 7 follows. Beetles contribute only slightly to the nucleus of perennial predominants in each stage (Smith, '28). There are no perennial predominant beetles in Stage I; 2 species are so classified in Stage II; in Stage III the condition is as in Stage I; while in Stage IV and in the climax forest two species appear in each list of perennial predominants. Since Fig. 7 represents the relative importance of seasonal forms to a great extent, it is to be expected that a large number of species are involved. The following discussion gives an idea of the diversified nature of the beetle population.

In the pioneer presocies two of the eight species of beetles present in the vernal socies, *Apristus subsulcates* Dej. and *Agonoderus comma* (Fab.), have been included in the group of subinfluent seasonals. Of the fourteen species present in the estival socies, only three species *Anthicus sturmi* Laf., *Systena taeniata* var. *blanda* Melsh and *Phyllotreta sinutata* (Steph.), were present in every collection during the estival season and in sufficient numbers to warrant them being considered as influent seasonals; while *Psylliodes punctulata* Melsh appeared in abundance in the early weeks of the socies but disappeared from the samplings of the last two weeks. Consequently, the last is included only as a subinfluent seasonal of the presocies. The serotinal socies shows the lowest peak of the presocies, 30.9 per cent (77 individuals per square meter), but has the largest number of species. Twenty-three species are taken in the collections, of which number only seven have appeared previously in the pioneer presocies. Only one species, *Hypnoides pectoralis* (Say), an elaterid beetle, had a sustained abundance throughout the socies sufficient to cause it to be considered as an influent seasonal.

Stage II on the clover-covered ridges shows a high prevernal and vernal beetle population while a series of peaks and depressions are evident throughout estival and serotinal socies until August 9 (Fig. 7). From this time until the close of the socies, the beetle population becomes increasingly more abundant until a peak of 54.0 per cent (184 individuals per square meter) is reached on August 30. The autumnal socies (1925) shows a fluctuating population, with a decline near its close. The list of 31 species present in the estival socies showed only *Systena hudsonias* (Forst.) and *Epicauta mar-*

ginata Fab. of subinfluent seasonal rank. Stages III and IV show peaks in late vernal and early estival socies, respectively, and both have peaks in the late serotinal socies. Two of the 57 species of beetles recorded for the forest edge are considered of influent seasonal rank; while the 76 species of the flood plain forest show one species of influent and eleven species of subinfluent seasonal rank. The autumnal socies (1925) of the flood plain forest has the highest beetle population of the presocies (256 individuals per square meter). The presence of a large number of beetles in the autumnal socies and their absence in the prevernal socies would indicate an unsuccessful attempt to hibernate in the flood plain forest stage.

During February, March, and April there is a sustained abundance of beetles in University Woods (presociety), ranging from 336 to 792 individuals per square meter, with a decline to 48 individuals per square meter by June 21 (Fig. 7). Weekly collections at Brownfield Woods did not begin until the last of May so the early societies cannot be compared. Brownfield Woods has a single peak in the estival society followed by a gradual decrease at the close of the society. During the early serotinal society the beetle population at Brownfield Woods is always less than in University Woods, but rises higher in the late serotinal society. The autumnal society (1925) shows no increase in the number of species present but a distinct difference in taxonomic composition and an increase in the number of individuals. Seventy-six species of beetles were recorded for the climax units, only seven species being different for the two units. Eight species were listed as seasonal influents, and five species as subinfluents (see Smith, '28, Tables I-V, for names of species not given here).

The graphs of beetles, mites, Diptera and cicadellids (Figs. 7-10) show the relative abundance of groups largely of seasonal importance. The graphs of ants and earthworms give groups which are more perennial than seasonal in their influence. From the point of view of contrast in stability between preclimax and climax groups it is interesting to note that all seasonal groups are more important relatively in the earlier stages than in the climax forest. The various presocies are made up of groups which contribute largely to the composition of the community. At some period in every subclimax stage, some one group of animals makes up over 40 per cent of the entire population, with the exception of Stage IV, where 33 per cent is the highest contribution of any one group with the exception of the earthworms. In the climax stage, however, no one group of animals makes up more than 25 per cent of the total population at any time, with the exception of the earthworms. Earthworms are more abundant in the climax stage as contrasted with ants which have a higher percentage abundance in the subclimax stages. In general, then, the climax is made up of a large number of groups each contrib-

uting a smaller percentage of the total population, while each group of the presocies contributes more largely to the total population.

THE SERAL FREQUENCY OF OCCURRENCE OF QUANTITATIVELY IMPORTANT GROUPS OF ANIMALS

During June, July, and August of 1926 weekly quantitative samplings of the animal populations were made in all five stages of the sere, under weather conditions as nearly alike as it was possible to select for a given set of collections, and with the schedule so arranged that the hours of sampling were somewhat equalized for the different stages. An analysis of populations on the basis of taxonomic groups present can be made during this time with results which should be quite comparable. Table I suggests a new interpretation of the composition of the communities of a sere, when they are analyzed in terms of the larger taxonomic groups present and the changing importance of these groups with succession. Frequency of occurrence was obtained by taking the total number of individuals of a given taxonomic group present in all of the collections of the period and finding their percentage of the total population for that period. For example, the total number of individuals collected during June, July, and August in Stage V (University Woods) was 26,898, while the total spider population taken for the same time was 3,577 individuals, which gives 13.3 per cent of spiders.

Populations analyzed in this way for the pioneer presocies (Table II) show 27.5 per cent of beetles present, which is almost 10 per cent more than any other group in Stage I and 6.7 per cent greater than for any other group of animals taken in any seral stage (ants are 20.8 per cent in Stage II). Beetles occupy third place in Stage II with 12.8 per cent abundance; they rank fifth in Stage III with 8.1 per cent abundance; fourth in Stage IV with 11.1 per cent abundance; and fourth in Stage V at 8.5 per cent. Ants have the highest frequency of occurrence in Stages II and III, with percentages of 20.8 and 13.7 respectively; while they rank third in Stage I with 13.2 per cent abundance; in Stage IV they are seventh in position with 3.7 per cent abundance; and in the climax stage they rise to fifth position with a percentage of 6.4.

Table II clearly shows the fact that taxonomic groups have a very different frequency of occurrence in the several stages of the woodland sere. Table III illustrates the variability in occurrence and the quantitative importance of six of these animal groups which are either first or second in position in one or more of the seral stages. The arrangement of the groups in the table follows the order of their position in the sere. At a glance it is seen that spiders show highest seral abundance, with a frequency of occurrence which varies from 10.7 to 20.6 per cent of the total population in the different seral stages. Collembola and earthworms hold first rank in the climax stage,

where they form 35.5 per cent of the population. They decrease in rank and percentage from climax to pioneer stage, with earthworms disappearing from the samples of the pioneer stage and Collembola occurring in eleventh position with a percentage of 1.3. This arrangement tends to equalize the groups in their relationship to the sere as a whole, for it shows readily that although Collembola and earthworms are very abundant in the later stages, they have a far greater variability of occurrence than the other four taxonomic groups. When this comparison is made, it becomes evident that the seral importance of any group of animals is dependent upon its relative position in the stage as well as its percentage of the total population.

SERAL DISTRIBUTION OF TOTAL SPIDER POPULATIONS

The presence of spiders in all seasons and their relatively great abundance in all seral stages, makes them an interesting form for comparisons. Seral distribution of total spider populations, analyzed in terms of their biotic significance in presocies or presociety (their abundance in relation to the total population of the community), and their relationship to community structure (occurrence as perennial and seasonal predominants), is shown in Fig. 12.

Spiders rank second in abundance in the pioneer presocies (Table II) with 52.9 individuals per square meter. The maximum spider population for the year is found in the vernal socies (Fig. 12), when 59.1 per cent of the population (107 individuals per square meter) consists of spiders. The autumnal socies has the second highest peak of the year, only 6.0 per cent less than the high vernal peak. *Dictyna bostoniensis* Em., *Lycosa* sp., *Phrurolithus sp.*, and *Cicurina* sp. are the perennial predominants of the pioneer presocies, and *Xysticus* sp., *Pardosa* sp., *Bathyphantes formica* Em., *Misumenops asperatus* Htz., and *Tetragnatha laboriosa* Htz. are the seasonals. The perennials are the most abundant in the vernal socies, and the seasonals in the serotinal socies.

The clover-covered ridges have the lowest spider population of the succession. Instead of an interseasonal depression, there is a rise to the peak of the presocies between estival and serotinal socies when 21.1 per cent (112 individuals per square meter) is reached. The autumnal socies (1925) has an increase in spider population, followed by a rapid decline in numbers during the early hiemal socies. Of the fifty-six species appearing in the collections of Stage II, only two species, *Linyphia mandibulata* Em. and *Drassodes robustus* Em., occur as perennial predominants, and *Tetragnatha* spp., *Hahnia* sp., *Misumenops* spp., *Diplocephalus crigonoides* Em., *Araneus arabescus* Walck., and *Lycosa* sp. as seasonals.

Spiders show their highest per cent of frequency in the forest edge presocies (III), during late prevernal and early vernal socies (Fig. 12), when both perennial and seasonal predominants have a comparatively high abun-

dance. *Theridion frondeum* Htz. is the perennial predominants of the presocies, and *Argiope aurantia* Lucas, *Argiope trifasciata* Forsk., *Tetanura* sp., *Oedothorax flaveolus* Bks., *Tetragnatha laboriosa* Htz., *Lycosa* sp., *Araneus arabescus* Walck., *Mangora gibberosa* Htz., and *Bathyphantes zygios* Keys are seasonal predominants. Spider population rises throughout autumnal and early hiemal socies.

Prevernal and vernal populations for Stages III and IV are much the same (Fig. 12), although the flood plain forest (IV) has a slightly lower peak. Following the vernal depression in Stage IV, there is a gradual increase, with minor fluctuations and excepting the interseasonal depression, to 39.0 per cent (358 individuals per square meter) during the first week of August. The population decreases in the autumnal socies but rises again in the early hiemal socies. *Theridion frondeum* Htz. is the perennial predominant of this presocies, and *Mangora gibberosa* Htz., *Linyphia clathrata* Sund., *Agroeca* sp., *Tetragnatha laboriosa* Htz., *Oedothorax flaveolus* Bks., and *Bathyphantes* sp. are the seasonal predominants.

The presociety (University Woods) has a prevernal peak of 21.5 per cent (366 individuals per square meter), when seasonals are abundant in the collections (Fig. 12). Following the appearance of the prevernal seasonals, the perennials are much less abundant than the seasonals during the remainder of the observations. *Xysticus* sp., *Anyphaena rubra* Em., and *Tetragnatha* sp. are the perennial predominants of the climax stage. The seventy-six species of spiders collected show only the following seasonals: *Gongylidiellium pallidum* Em., *Phrurolithus palustris* Bks., *Mangora gibberosa* Htz., *Micrathena gracilis* Walck., *Hahnia agilis* Keys., *Agelena naevia* Walck., *Oedothorax flaveolus* Bks., *Ceraticelus* sp., *Lycosa* sp., *Agroeca* sp., *Dictyna* sp., *Microneta* sp., *Bathyphantes zebra* Em., and *Cicurina arcuata* Keys.

Spiders bear a different relationship to the total populations in the various seral stages as shown by their changing taxonomic composition and numerical abundance. They are relatively more abundant in the pioneer and in the flood plain forest stages (I and IV) and make up a greater proportion of the predominants of these stages, while Stages II, III and V have a greater percentage of seasonal forms.

SERAL DISTRIBUTION OF TOTAL INVERTEBRATE POPULATIONS

Presocies and presociety undergo a series of changes during the year which are caused by the addition of successive seasonal predominants to the ever present nucleus of perennial predominants. These changes are shown by fluctuations in the total populations. Figure 13 compares the total invertebrate populations of the seral stages, from February 22 to September 6, 1926 and indicates the relationship existing between the seasonals and the perennials as shown by their percentage of the total populations. Strata are

ignored, and the totals (tree stratum omitted) are based upon the number of animals collected in all strata of presocies of presociety. The percentages have been computed upon the basis of the largest number of animals taken in any collection during the period of the observations. This was 4,627 individuals per square meter at Brownfield Woods on August 16, 1926. Using this figure as 100 percentage, the number of animals of each sampling has been converted into a percentage of the total for this highest population of the sere.

The absence of a ground covering, and heavy rains in the autumn and early spring prevent animal species from living above the ground or at the ground surface during the hiemal socies of the pioneer presocies. A continuous rise in total population occurs from the appearance of animals above ground in the early vernal socies until the peak of the year is reached on June 28, with a population of 528 individuals per square meter (Fig. 13). The autumnal socies (1925) has the second highest peak of the year when the population rises to 509 individuals per square meter.

Lepidopterous larvae were found over-wintering in the dried clover stalks of Stage II, and an occasional nest of grasshopper eggs was dug up. Beetles and spiders appear in the upper 10 cm. of soil during the prevernal socies, followed by a continuous rise in population until the close of the vernal socies, when a total of 518 individuals per square meter are taken (Fig. 13). The maximum peak for the stage of 20 per cent (925 individuals per square meter) occurs on July 12, which is two weeks later than the maximum of the pioneer stage.

Stages III and IV of the artificial flood plain forest sere are located along the Salt Fork River, with the result that a layer of silt and sand may be deposited over the surface of the ground during seasons of heavy rain and high waters. This condition was so marked during the winter of 1925-1926 that the fallen leaves were buried to a depth of several inches, making a satisfactory hiemal study impossible. The early prevernal socies of Stage III had a small population of spiders, mites, ants and earthworms, with a distinct increase in the population of the vernal socies when a peak of 17.5 per cent (810 individuals per square meter) is reached on May 29, 2.0 per cent less than the peak of August 16, which is the maximum for the year. The maximum peaks of Stages II and III occur in estival and serotinal socies respectively, and at no time does the population percentage of the forest edge stage quite attain that of Stage II, while the seasonal peaks of Stage III are more prominent than those of either of the preceding stages, appearing distinctly in vernal, estival and serotinal socies. The flood plain forest stage has the highest population of the stripland stages, with the maximum population for the year present in the early estival socies when 24.5 per cent (1,134 individuals per square meter) were taken in the samplings. The autumnal

socies (1925) has a peak of 20.6 per cent, when spiders and beetles are abundant in the collections.

Autumnal and hiemal societies (1925) of the presociety show considerable weekly fluctuations in total populations when hibernating forms as Cicadellidae, beetles, and spiders become prominent in the collections as they migrate inward and downward (Weese, '24); when they reappear in the samples on warm winter days; or when *Enchytraeidae* and Collembola have a marked increase in abundance during times of greater moisture. The prevernal society has 94.3 per cent (4,363 individuals per square meter) population near its close, while the vernal society shows a continued rise to 99.4 per cent when a great number of *Enchytraeidae* and Collembola are taken in the ground collections. The weekly collecting schedule for Brownfield Woods did not commence until the vernal society was established, which prevents a comparison of these two units during the prevernal society. However, they show the similarity of relatively low estival populations; both have a marked decline interseasonally; and each rises to a high peak in the serotinal society. Brownfield Woods has the maximum peak for the sere with 100 per cent (4,627 individuals per square meter) population on August 16, 1926.

A biometrical analysis of the weekly fluctuations in the total population of each seral stage brought out the following facts with reference to the degree of variability in these fluctuations:

TABLE I

Significance of variability in total population

Stage	Mean Weekly Population in Percentage[3]	Standard Deviation in Percentage	Coefficient of Variation[4]
I	5.8 ± 0.460	2.46 ± 0.325	42.4 ± 6.54
II	10.5 ± 0.860	4.94 ± 0.608	47.0 ± 6.96
III	10.4 ± 0.854	5.07 ± 0.604	48.7 ± 7.05
IV	13.7 ± 1.111	6.59 ± 0.786	48.1 ± 6.93
V	59.9 ± 4.718	27.09 ± 3.336	45.2 ± 6.61

Although the weekly populations in Stage V fluctuate more widely than do the weekly populations in any other stage of the sere (Fig. 1), the percentage fluctuation or variability within the weekly populations of Stage V as measured by $\frac{\sigma 100}{m}$ = coefficient of variation, is practically the same as in any of the other stages of the sere. The coefficient of variation reduces the variability in the weekly populations in the various stages to a common basis, percentage basis, for comparison. σ in the above formula represents the

[3] The numerical mean weekly population may be determined by multiplying the percentage mean by 4,627 which is the 100 per cent basis.

[4] Coefficient of Variation $= \frac{\text{Standard Deviation} \times 100}{\text{mean}}$

standard deviation in the weekly populations in any stage and is a measure of variability within these populations. ^{m} represents the arithmetic mean of the number of individuals composing the weekly populations, or in other words, is the mean weekly population of the stage. Hence as the number of individuals composing the weekly populations increase, the variability or degree of fluctuation within these populations increase but in such a manner that the relation between them as measured by $\frac{\sigma^{100}}{m}$ =coefficient of variation tends to remain constant. This, however, is no more than is to be expected under the existing conditions, since the population growth function (Lotka, '25; Wright, '26; Hotelling, '27) is of such a nature that environmental factors tend to have constant percentage effects rather than absolute effects upon the rate of growth of animal populations. Consequently, it seems probable that life cycles are of corresponding occurrence in the various stages and greatly influence the rate of growth of the total animal population within each stage. As succession progresses, however, more stable conditions develop and a changing relationship is seen among the forms composing the populations. The climax forest has a more uniform population which consists of a smaller percentage of incidental and seasonal species, and a larger number of perennial predominants.

DISCUSSION AND CONCLUSIONS

Food chains and food relations have usually been emphasized in the evaluation of species in communities. Food data are usually obtained from the literature. The basis of the records for the larger species lies in haphazard observation of stomach contents of specimens of unknown community relations. For the smaller species reports of food habits result from the observation of one species rarely repeated under the various conditions in which the species occurs and too often applied to related forms by inference. The literature concerned with the species treated in this paper was of little value. Exact information as to the food habits of the species found important hardly exists and time spent in searching for such information appeared wasted.

In the areas of study, the larger and more influent animals have either been exterminated or greatly reduced in numbers. This paper deals chiefly with arthropods of average size. Relative to this type it may be said that the biotic significance of an animal species within a community depends upon its abundance (having due regard for its size) in relation to the total population. The composition of the biotic communities of the woodland sere in the two years of study shows great variability in the frequency of occurrence of the important groups present.

In detail the conclusions may be summarized as follows:

1. The animal population of the seral stages and climax responded to differences and to variabilities in the weather conditions, namely rainfall, temperature, and humidity.

a. Different species reached their maximum abundance in two different years.

b. Species of one biotic season (*e.g.* estival) of 1925 appeared in the following biotic season (*e.g.* serotinal) in 1926.

c. Species abundant in one of the years were in some cases inconspicuous or wanting in the other.

2. Statistical examination of the data brings out the following facts:

a. The changing populations of the seral stages as indicated by the mean weekly catches from each stage, continually increase from the pioneer to the climax stage.

b. The relative variability within the total populations of the stages, as measured by the coefficient of variation of the weekly populations within each stage, remains practically constant throughout the entire sere.

c. The latter may be interpreted as due to the constant percentage effects of the climatic factors upon the rate of growth of the animal populations within the various stages.

3. The conclusions regarding the character of the climax and its comparison with the seral stages are as follows:

a. The climax maintains a cooler, moister and less variable microclimate than that of the subclimax stages which begin with the greatest extremes and gradually approach the climax condition.

b. The number of seasonal and incidental species decreases as succession proceeds and is least in the climax.

c. The number of perennial predominants increases toward the climax which is characterized by the largest number.

d. The presociety of the climax community is characterized by the presence of a large number of species, many of which became prominent in one or the other of the two years.

TABLE II. *Frequency of occurrence of animals quantitatively important in the woodland succession.*

STAGE I	%	STAGE II	%	STAGE III	%	STAGE IV	%	STAGE V	%
Beetles	27.5	Ants	20.8	Ants	13.7	Spiders	20.6	Collembola	18.0
Spiders	17.6	Aphids	14.7	Diptera	12.8	Diptera	18.9	Earthworms	17.5
Ants	13.2	Beetles	12.8	Cicadellidae	12.0	Collembola	12.9	Spiders	13.3
Mites	10.9	Spiders	10.7	Spiders	11.3	Beetles	11.1	Beetles	9.8
Hemiptera[6]	9.5	Mites	6.3	Beetles	8.1	Cicadellidae	8.3	Ants	6.4
Diptera	4.5	Hemiptera	6.2	Collembola	7.9	Earthworms	4.8	Mites	5.5
Grasshoppers	4.2	Diptera	5.6	Grasshoppers	6.4	Ants	3.7	Snails	5.0
Cicadellidae	2.4	Grasshoppers	3.7	Hemiptera	5.0	Mites	2.6	Diptera	3.6
Hymenoptera	2.0	Cicadellidae	3.4	Mites	3.0	Hemiptera	1.9	Hemiptera	3.7
Lepidoptera[7]	1.3	Millipedes	3.1	Lepidoptera	2.7	Hymenoptera	1.7	Millipedes	2.7
Collembola	1.3	Earthworms[8]	2.6	Tree-hoppers	2.8	Centipedes	1.5	Lepidoptera	1.8
Miscellaneous[9]	5.6	Lepidoptera	2.0	Earthworms	2.8	Tree-hoppers	1.3	Centipedes	1.8
		Hymenoptera	1.0	Hymenoptera	1.9	Lepidoptera	1.0	Cicadellidae	1.7
		Collembola	1.0	Aphids	0.7	Tree-crickets	1.0	Hymenoptera	1.3
		Centipedes	0.5	Centipedes	0.5	Snails	0.9	Miscellaneous	7.9
		Miscellaneous	5.6	Millipedes	0.5	Miscellaneous	7.8		
				Snails	0.5				
				Miscellaneous	7.4				
Total percentage	100.0		100.0		100.0		100.0		100.0
Total population	2,938		5,841		5,859		8,230		262898
Av. population per square meter	268		531		532		748		2,445

[6] Exclusive of those specifically listed elsewhere in the table.
[7] Includes both adults and larvae.
[8] Includes all earthworms, although *Enchytraeidae* and *Lumbricidae* furnish the higher percentage.
[9] Forms present discontinuously in the collections or furnishing less than 0.5 percent of the population.

Frequency of occurrence was obtained by taking the number of individuals of a given taxonomic group collected during June, July and August, 1926 (weekly collections) and finding their percentage of the total population for the same period.

TABLE III. *Variability in occurrence and quantitative importance of six significant animal groups.*

TAXONOMIC GROUP	STAGE I		STAGE II		STAGE III		STAGE IV		STAGE V		AV FOR SERE	
	P[10]	R. P[11]	P.	R.P.	P.	R.P.	P.	R.P.	P.	R.P.	P.	R.P.
Spiders	17.6	2	10.7	4	11.3	4	20.6	1	13.3	3	13.74	2.33
Ants	13.2	3	20.8	1	13.7	1	3.7	7	6.4	5	8.35	3.40
Beetles	27.5	1	12.8	3	8.1	5	11.1	4	9.8	4	7.87	3.40
Diptera	4.5	6	5.6	7	12.8	2	18.9	2	3.6	8	6.11	4.16
Earthworms	0.0	0	2.6	11	2.8	12	4.8	6	17.5	2	10.28	5.16
Collembola	1.3	11	1.0	14	7.9	6	12.9	3	18.0	1	12.60	7.00
Total population	2,938		5,841		5,859		8,230		26,898			
Average per square meter	268		531		532		748		2,445			

[10] Percentage in stage or sere.
[11] Relative position in stage or sere.

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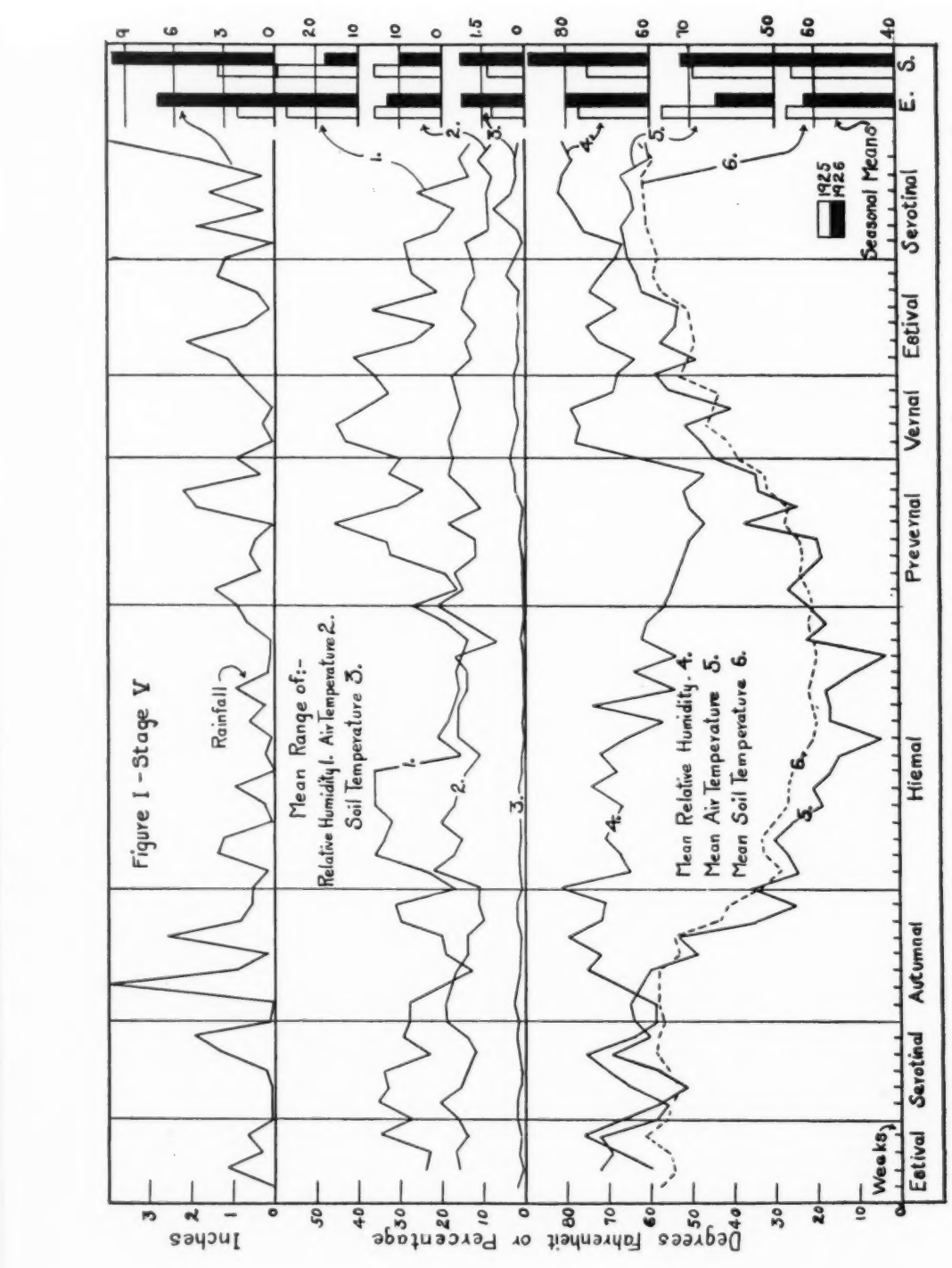


FIG. 1. Showing conditions of temperature, humidity, and rainfall from June 22, 1925 to September 6, 1926, in a maple-red oak climax forest (Stage V), Urbana, Illinois. Soil temperature (10 cm. below ground surface), air temperature and relative humidity (0.6 m. above ground), are measured by the use of thermographs and hygrograph, while rainfall data are taken from U. S. Weather Bureau records for Urbana, Illinois. Data are reported as weekly or seasonal mean (average of two-hourly readings for the week or season), weekly or seasonal means range (difference between the averages of daily maxima and of the daily minima for the week or season), and as weekly or seasonal rainfall in inches.

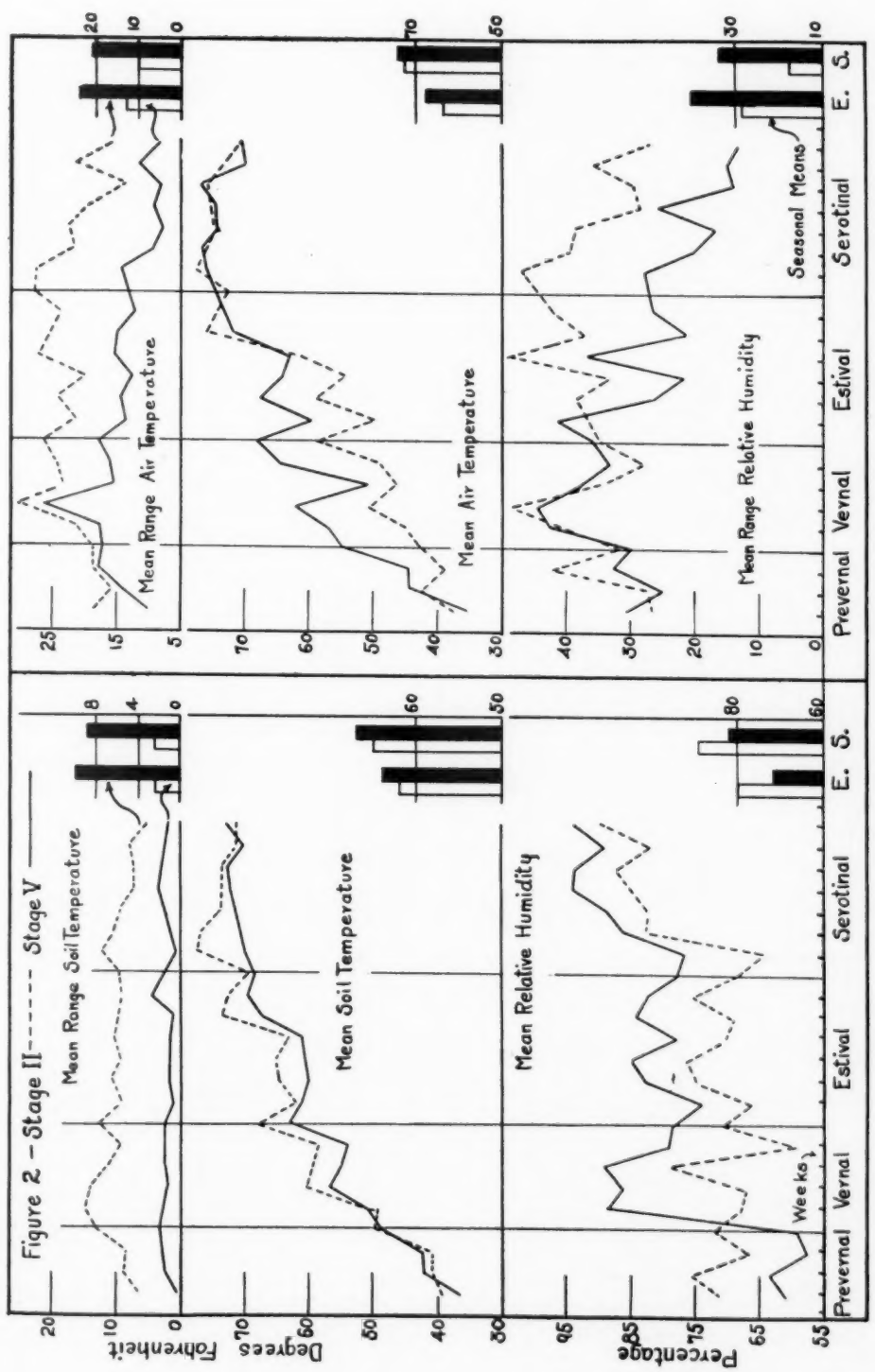


FIG. 2. Comparing conditions of temperature and relative humidity from March 22 to September 6, 1926, in Stage II (lower striplands, Vermilion County, Illinois), and in Stage V (University Woods, Urbana, Illinois) of a deciduous forest succession. Conditions measured and data reported as in Fig. 1.

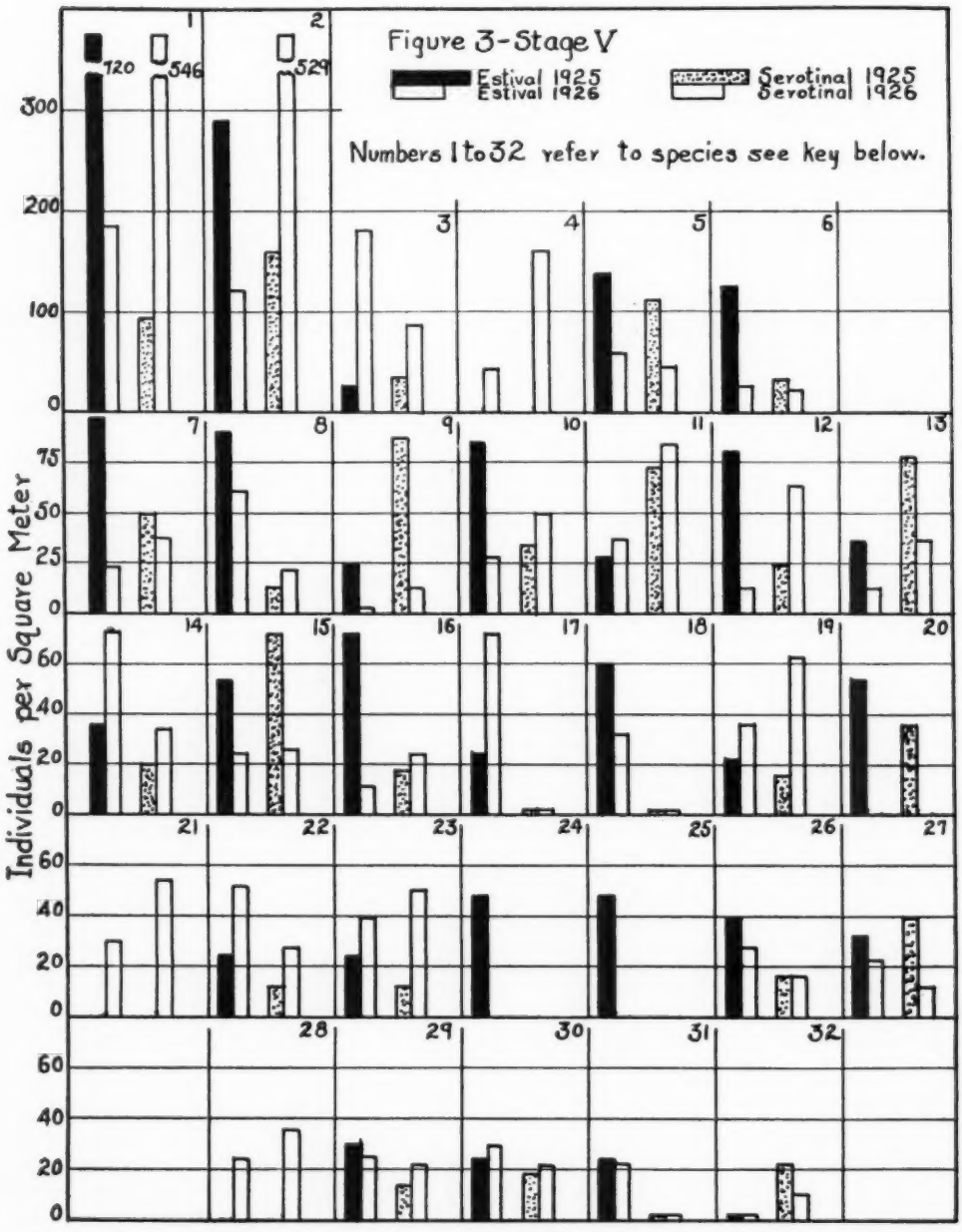


FIG. 3. Showing differences in the seasonal abundance of some invertebrate perennial and seasonal predominants of the climax maple-red oak forest (Stage V) of a woodland succession, during estival and serotinal societies of 1925 and 1926; University Woods, Urbana, Illinois. Abundance is given as seasonal mean (average of weekly collections). Species names and corresponding graph numbers are listed below:

1. *Enchytraeidae*[5] ..... Worm
2. *Tomocerus flavescens americana*[5] .. Springtail
3. *Parasitus* sp., Schött[5] ..... Mite
4. *Onychiurus subtenuis* Folsom .... Springtail
5. *Pokabius bilabiatus* (Wood)[5] ..... Centipede
6. *Aphaenogaster fulva* Roger ..... Ant
7. *Mangora gibberosa* Htz. ..... Spider
8. *Lasius niger americanus* Emery ..... Ant
9. *Oedothorax flaveolus* Banks ..... Spider
10. *Carychium exiguum* (Say)[5] ..... Snail
11. *Dicyphus gracilentus* Parsh[5] ..... Bug
12. *Lycosa* sp. ..... Spider
13. *Octolasium lacteum* (ö) ..... Worm
14. *Pseudogriphoneura crevecoeuri* Coq ..... Fly
15. *Formica* sp. ..... Ant
16. *Epuraea rufa* (Say) ..... Beetle
17. *Agroeca* sp. ..... Spider
18. *Leptothorax curvispinosus* Mayr ..... Ant
19. *Sapromyzosoma philadelphica* Macq .... Fly
20. *Phytonomus nigrirostris* Fab ..... Beetle
21. *Isotoma* sp. ..... Springtail
22. *Phrurolithus palustris* Bks ..... Spider
23. *Hahnia agilis* Keys ..... Spider
24. *Ptillodactyla serricollis* Say ..... Beetle
25. *Crematogaster lineolata* Say ..... Ant
26. *Erythroneura obliqua* Say[5] ..... Leaf-hopper
27. *Dictyna* sp. ..... Spider
28. *Microneta* sp. ..... Spider
29. *Xysticus* sp[5] ..... Spider
30. *Bathyphantes zebra* Em. ..... Spider
31. *Cicurina arcuata* Keys ..... Spider
32. *Cantharis excavatus* Lec. ..... Beetle

[5] Perennial predominant.

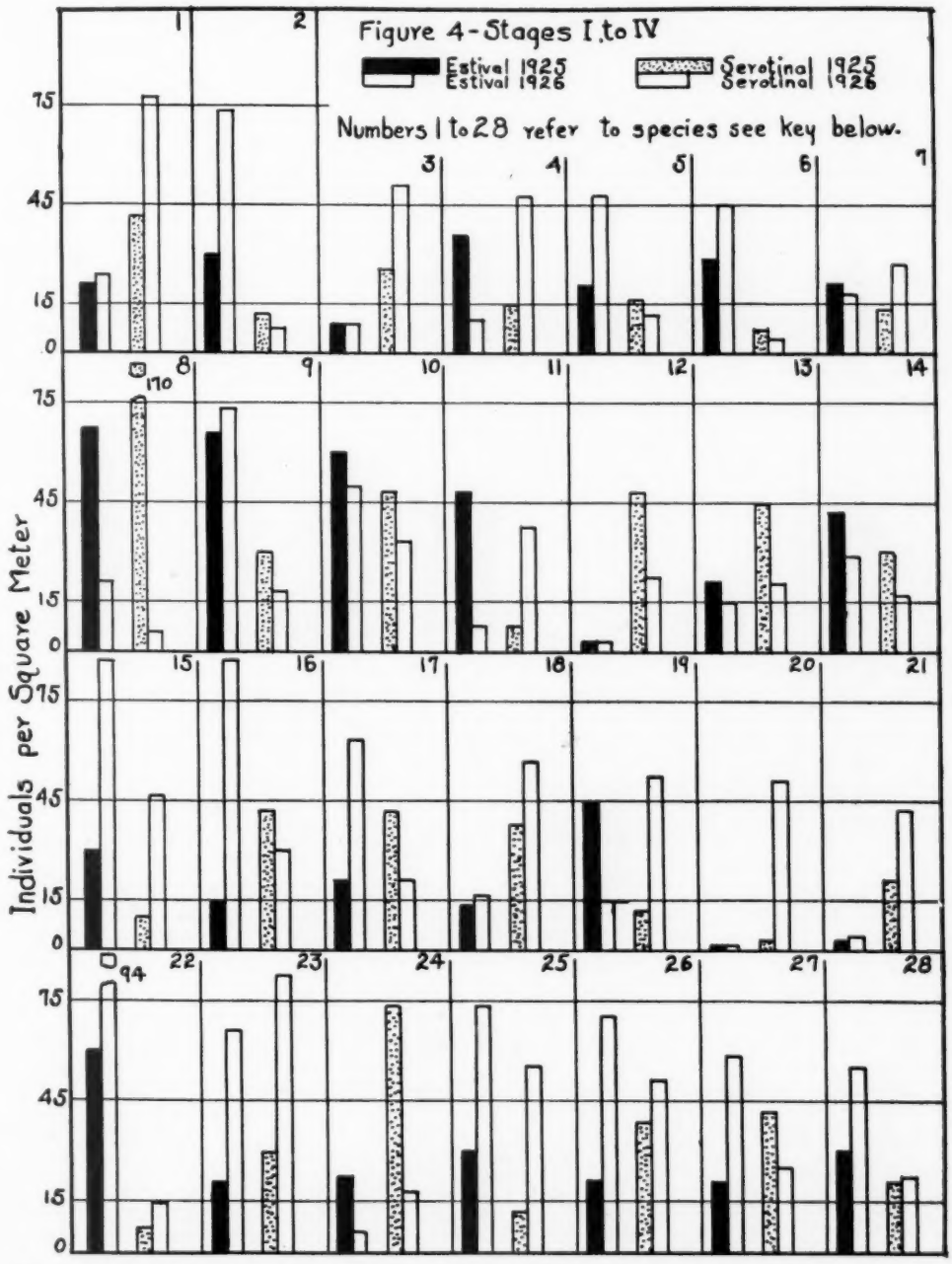


FIG. 4. Showing differences in the seasonal abundance of some invertebrate perennial and seasonal predominants of the developmental stages (I-IV) of a woodland succession, during estival and serotinal socies of 1925 and 1926. Lower striplands, Vermilion County, Illinois. Abundance is given as seasonal mean (average of weekly collections). Species names and corresponding graph numbers are listed below:

Stage I.

1. *Hypnoidus pectoralis* (Say).....Beetle
2. *Tarsotomus spinatus* Bks[5].....Mite
3. *Psylliodes punctulata* Melsh.....Beetle
4. *Aphaenogaster fulva* Roger.....Ant
5. *Anthicus sturmi* Laf.....Beetle
6. *Systena taeniata* var. *blanda* Melsh...Beetle
7. *Dictyna bostoniensis* Em[5] .....Spider

Stage II.

8. *Acyrthosiphon pisi* (Kalt).....Plant louse
9. *Melanoplus differentialis* (Thom.)...Locust
10. *Triphleps insidiosus* Say[5].....Bug
11. *Phymata erosa* L.....Bug
12. *Diplocephalus crigonoides* Em.....Spider
13. *Formica fusca argentata* Whlr[5].....Ant
14. *Chactocnema confinis* Cr.[5].....Beetle

Stage III.

15. *Euscelis comma* V. D.[5].....Leaf-hopper
16. *Chloropisca glabra* Mg.....Fly
17. *Camptoprosopella vulgaris* Fitch.....Fly
18. *Melanoplus femur-rubrum* DeG.....Locust
19. *Scolops sulcipes* Say.....Lantern-fly
20. *Erythraeus brevitarsus* Ewing .....Mite
21. *Botanobia salina* Curr.....Fly

Stage IV

22. *Anthomyza variegata* Lw.....Fly
23. *Camptoprosopella vulgaris* Fitch.....Fly
24. *Oedothorax flaveolus* Bks.....Spider
25. *Cicadellidae* spp. .....Leaf-hopper
26. *Theridion frondeum* Htz[5].....Spider
27. *Aedes vexans* Meigen.....Mosquito
28. *Pelastoneurus vagans* Lw.....Fly

[5] Perennial predominant.

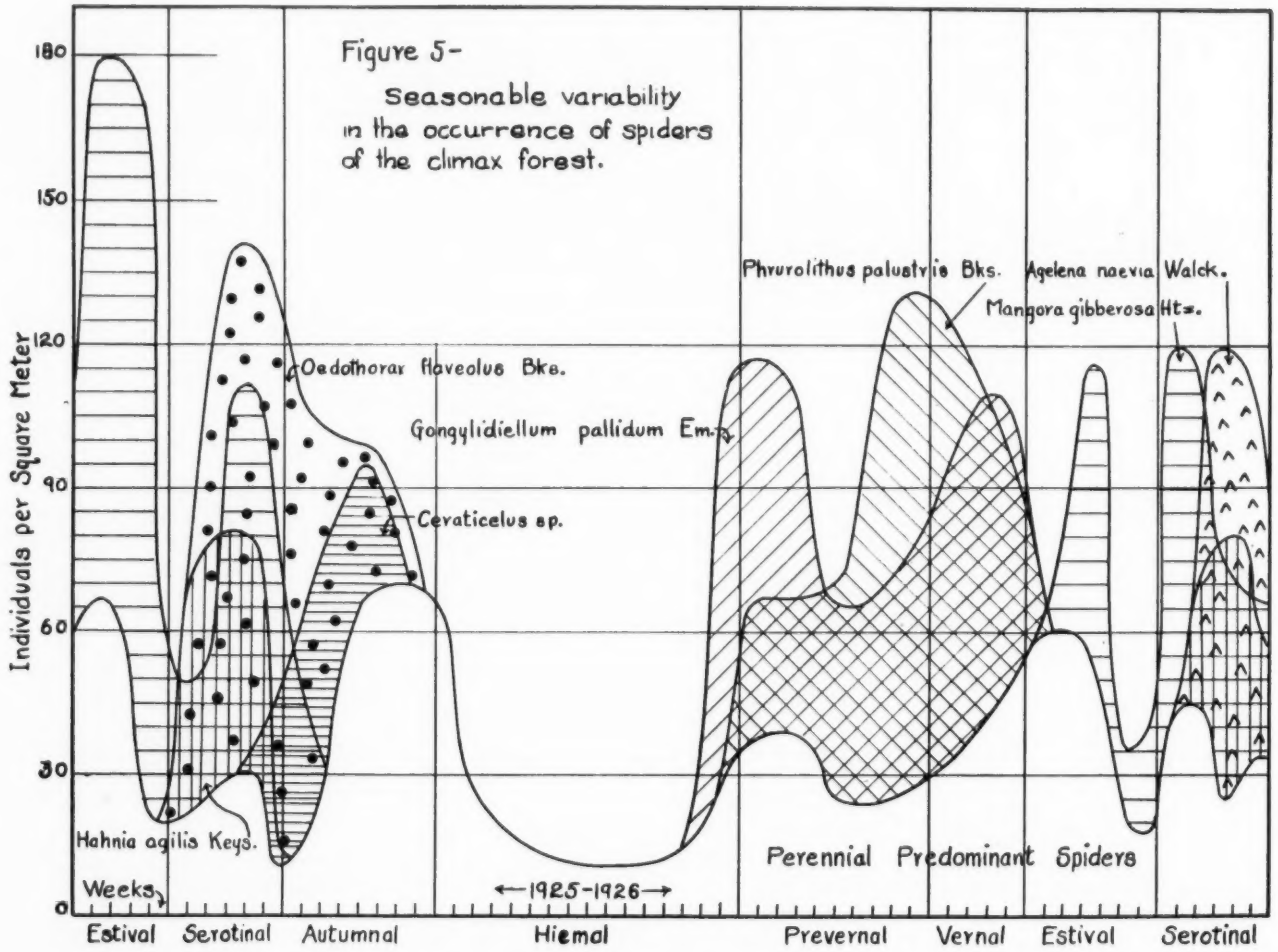
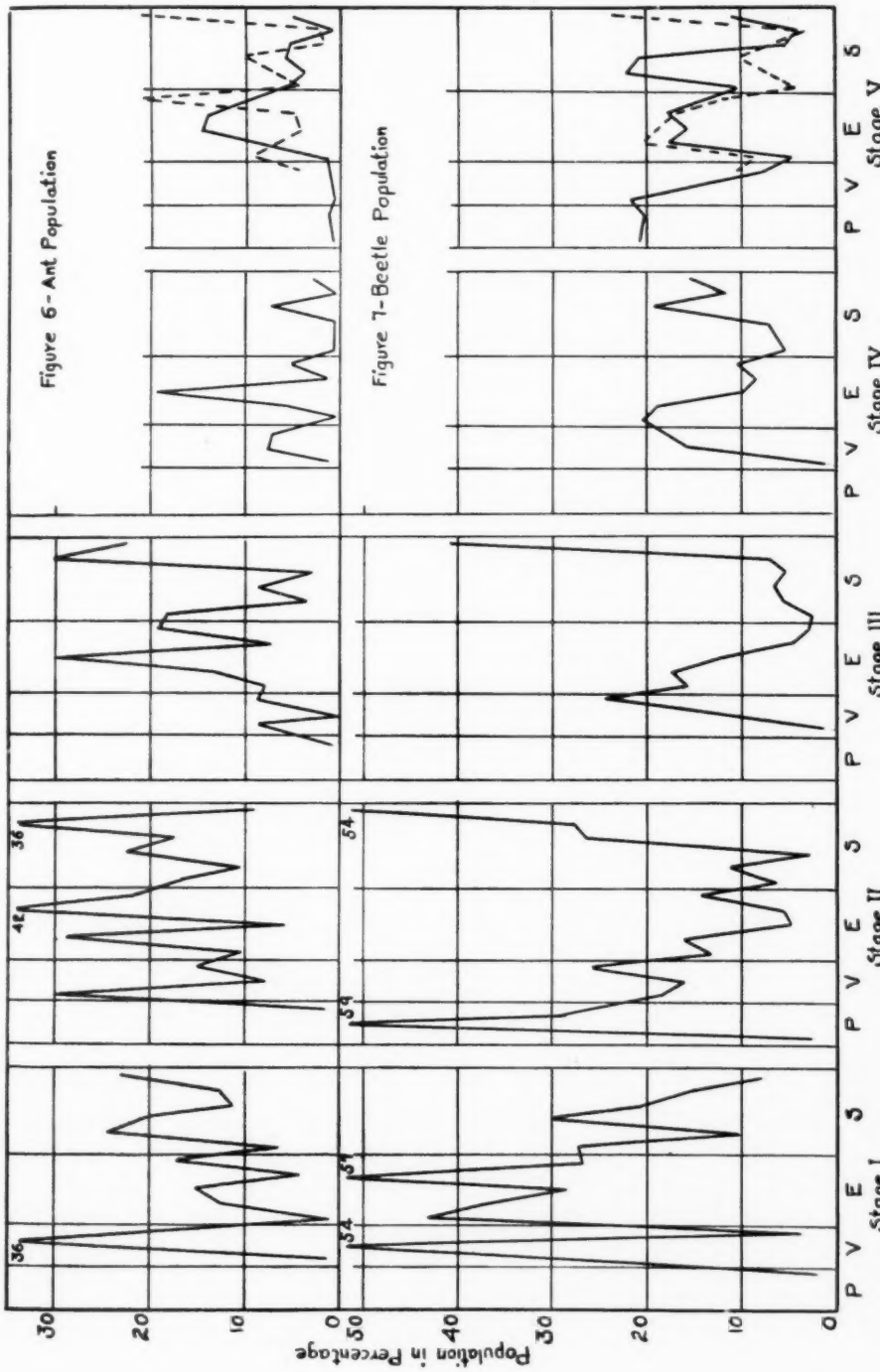


FIG. 5. Showing seasonal fluctuations in the abundance of perennial and seasonal spiders of the climax maple-red oak forest (Stage V) of a woodland succession, from June 21, 1925 to September 6, 1926. The curve formed by the frequencies of the perennials throughout the season forms the base (x axis) upon which the seasonals are plotted.



FIGS. 6 TO 11. Showing community relations of six animal groups, conspicuous in the invertebrate populations of the sere from February 22 to September 6, 1926. The abundance of species is given in terms of their percentage relationship to the total population of the same seral stage and date. Both climax units are included under Stage V, where the solid line represents University Woods and the dotted line is used for Brownfield Woods. The letters at the bottom apply to the biotic seasons.

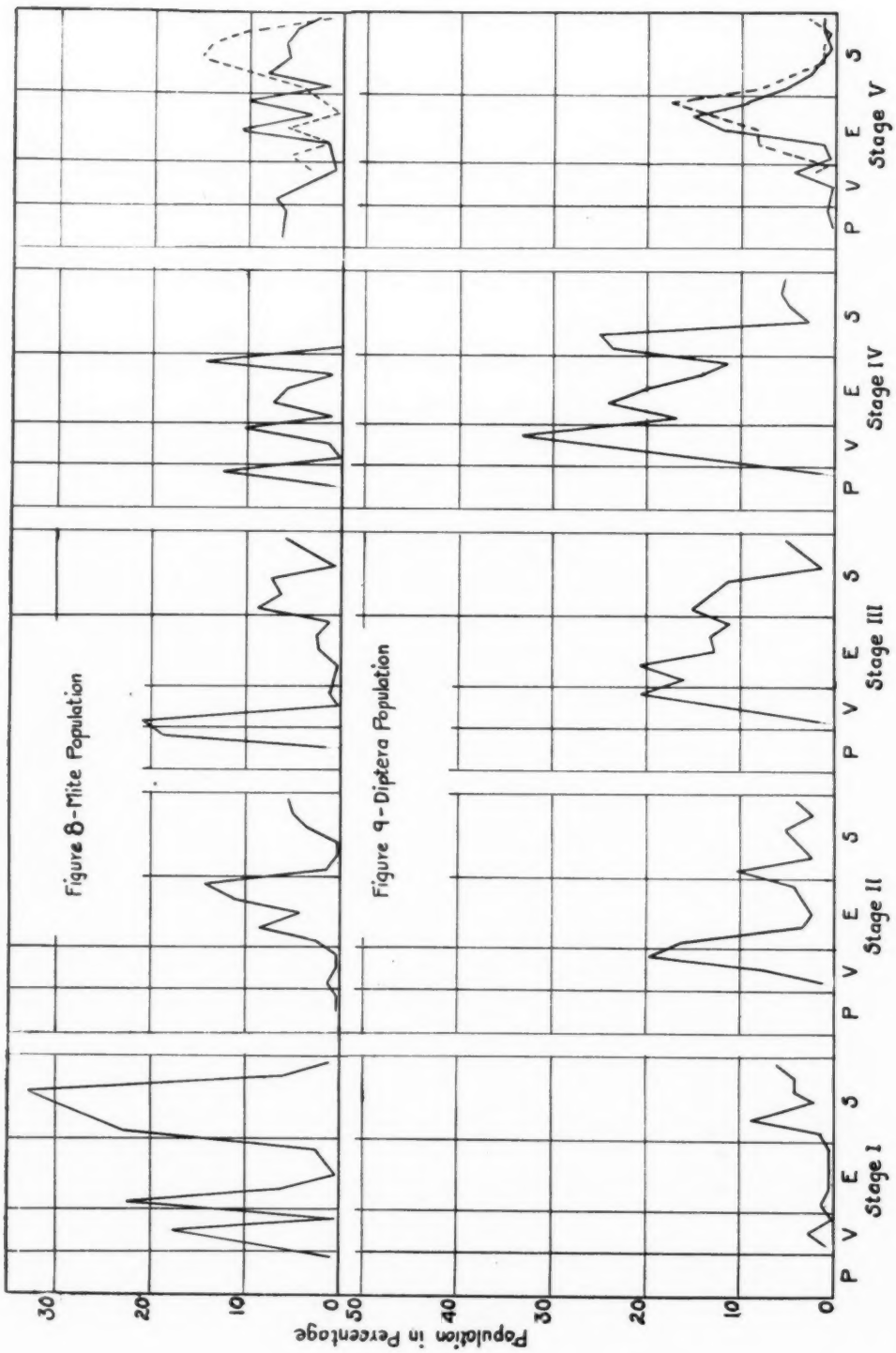


Figure 8-Mite Population
Figure 9-Diptera Population
Population in Percentage
30
20
10
0
50
40
30
20
10
0
P V E S
Stage I
P V E S
Stage II
P V E S
Stage III
P V E S
Stage IV
P V E S
Stage V

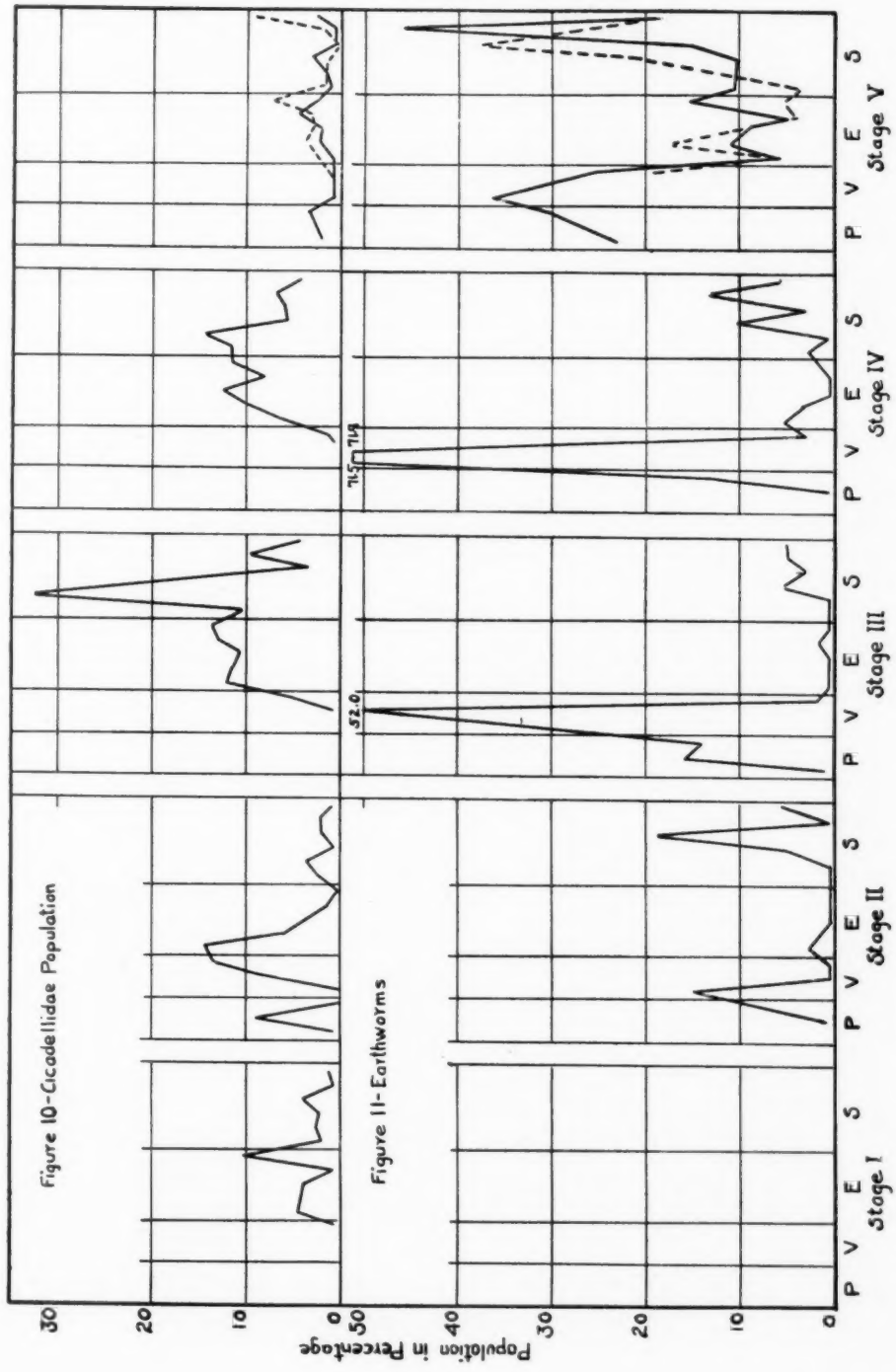


Figure 10-Cicadellidae Population
Figure 11-Earthworms
Population in Percentage
0
10
20
30
40
50
P V E S
Stage I
P V E S
Stage II
P V E S
Stage III
P V E S
Stage IV
P V E S
Stage V

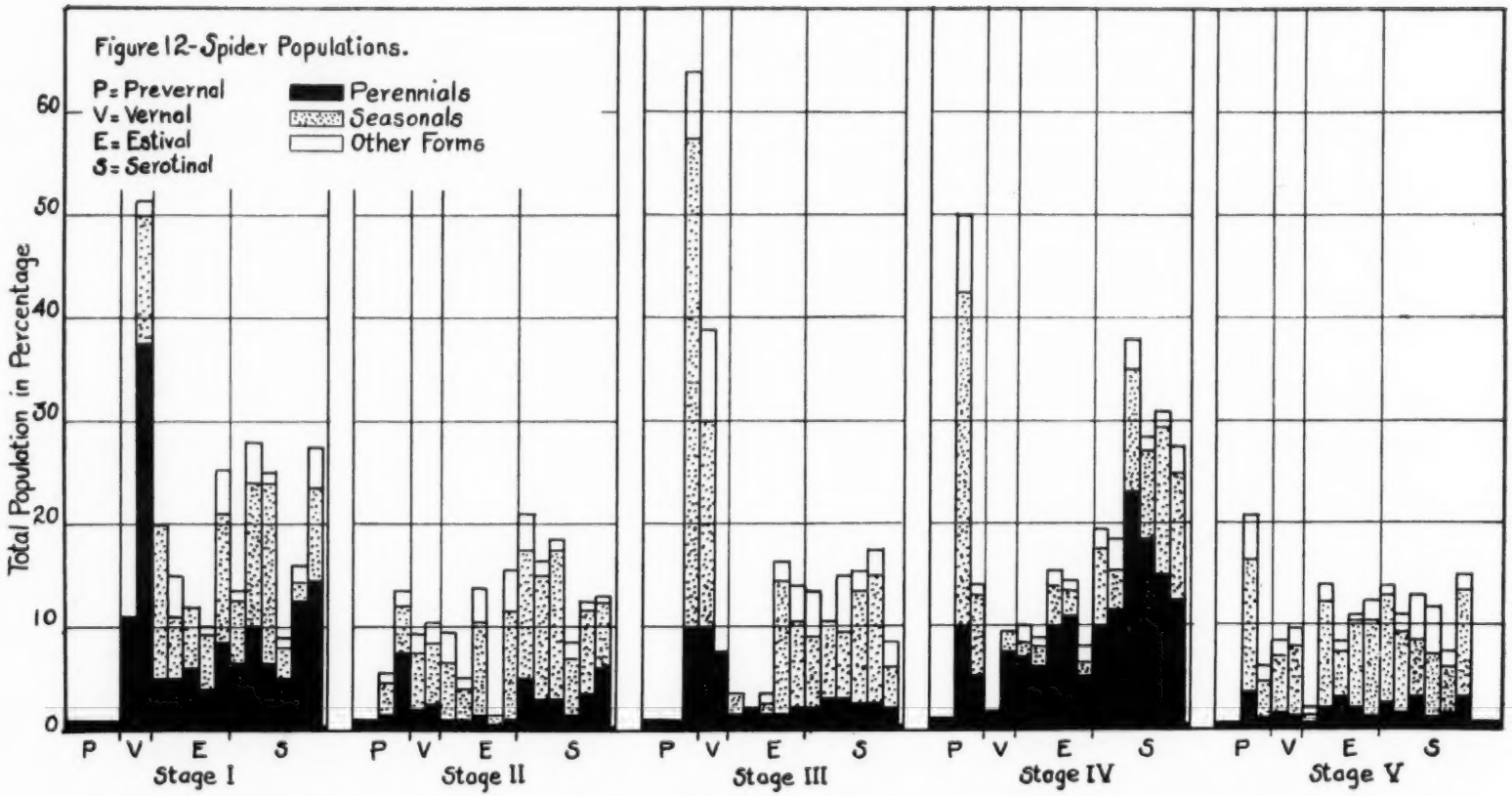


FIG. 12. Showing seral distribution of total spider populations from February 22 to September 6, 1926 in a deciduous forest succession. Developmental stages (I-IV) are located in the lower striplands of Vermilion County, Illinois, and the climax stage (V) is the maple-red oak forest of University Woods, Urbana, Illinois. The frequencies of the perennial predominants, represented by the solid polygons, form the base upon which the frequencies of the seasonal predominants are plotted. Likewise, the frequencies of other forms, showing less importance in the collections, are plotted upon the polygons of the seasonals.

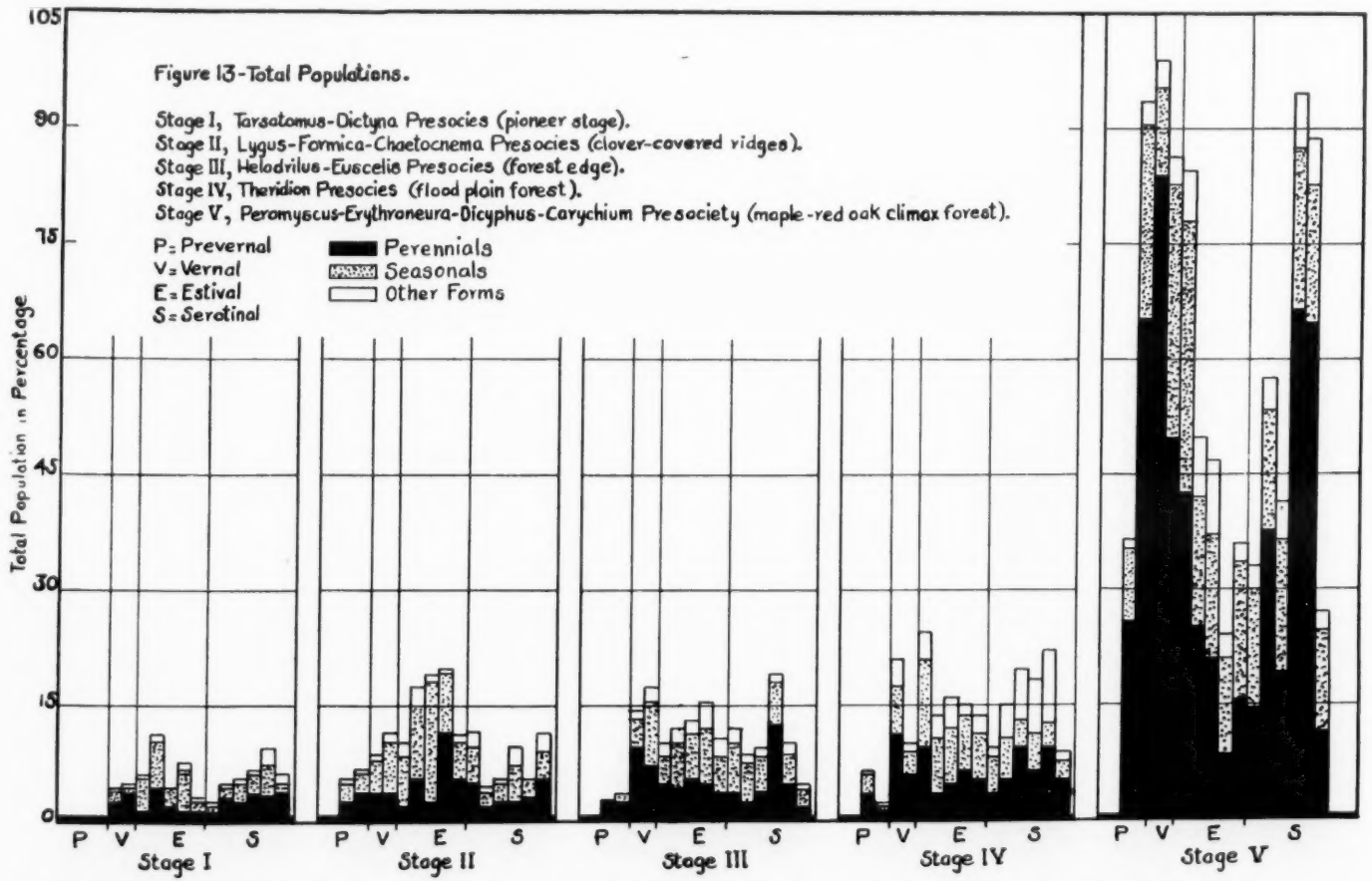


FIG. 13. Showing distribution of total invertebrate populations from February 22 to September 6, 1926 in a deciduous forest succession. The developmental stages (I-IV) are located in the lower striplands of Vermilion County, Illinois and the maple-red oak climax forest is University Woods, Urbana, Illinois. The number of animals of each sampling has been converted into a percentage of the total for the highest population of the sere—4,627 individuals per square meter at Brownfield Woods on August 16, 1926. The frequencies of the perennial predominants, represented by the solid polygons, form the base upon which the frequencies of the seasonal predominants are plotted. In like manner, the frequencies of other forms, less conspicuous in the collections, are plotted upon the polygons of the seasonals.

ATLANTIC COASTAL PLAIN PLANTS IN THE SAND BARRENS OF NORTHWESTERN WISCONSIN

By

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ATLANTIC COASTAL PLAIN PLANTS IN THE SAND BARRENS OF NORTHWESTERN WISCONSIN

INTRODUCTION

It has long been known that many plants of the Atlantic coastal plain have inland extensions of range and occur in places about the Great Lakes rather abundantly. Harper ('05) lists 41 species and genera which extend westward about the Great Lakes. He remarks, moreover, that of the coastal plain plants which occur in New England most extend not only southward along or near to the coast but also westward to Minnesota or thereabouts, the northern part of their ranges coinciding approximately with the area of glacial drift. Later Peattie ('22), making a detailed study of the occurrence of coastal plain plants in the Great Lakes region, found 90 species and varieties with this inland range. Peattie assumed, on the basis of the climatic and topographic features of the Lake Superior basin, that this region would not favor the occurrence of the coastal plain species, an assumption, for the most part, borne out by the facts. Peattie was not, however, aware that a considerable number of these species which are present so abundantly in the dunes area at the head of Lake Michigan, also extend westward into southern Wisconsin and into the sand barrens of northwestern Wisconsin as well as into adjacent areas of Minnesota.

Echinochloa Walteri, Eleocharis interstincta, Polygonella articulata, Nelumbo lutea, Polygala cruciata, Utricularia gibba, and other species of the coastal plain, in southern Wisconsin appear to occur on the shores, or in the waters of lakes which are recognized as being of glacial origin, and at the present time mere relics, in some instances, of larger glacial lakes. It was with this fact in mind that Dr. N. C. Fassett of the University of Wisconsin made a collecting trip into the northwestern part of the state in 1927 and again in 1928. On the broad sand beaches of the numerous lakes in Polk, Burnett, Douglas, Bayfield, Washburn, and adjacent counties were found *Juncus balticus* var. *littoralis, Panicum albemarlense, P. meridionale, Muhlenbergia uniflora, Stenophyllus capillaris, Rynchospora capitellata* (*R. glomerata* of Gray 7th ed.), *Xyris torta* (*X. flexuosa* of Gray 7th ed.), and *Polygonella articulata.* Not all the lakes had the coastal plain plants, however, and those which did were the lakes with the broad sand shores. Many of these lakes, moreover, had higher abandoned beaches, in many instances with bars and dry lagoons preserved. These facts suggested the possibility that the lakes were relics of a once larger body of water.

For four seasons, and in part contemporaneously with these botanical investigations, parties of the Wisconsin Geological Survey were investigating the area and accumulating geological evidence which led to the conclusion that

a large pro-glacial lake had covered the greater part of the area now known as the Sand Barrens. This lake was, accordingly, called the Barrens Lake. The result was a joint paper on the geological and botanical evidences for the existence of the lake (Aldrich and Fassett, '29). More recently Hansell ('30) has studied in greater detail the glacial geology of the region and the geological aspects of the lake.

Dr. Fassett turned the further investigation of the flora of the region over to the writer, and a joint field trip of six weeks was made in August and September, 1929. The writer supplemented these 1929 collections and field studies with further work in the field during the fall of 1930 in company with Dr. G. O. Cooper of the University of Wisconsin. In all, collections and ecological and distributional data from over 200 lakes within the area formerly occupied by Barrens Lake and in adjacent areas have been taken.

In addition to the collections of Dr. Fassett and the writer the collections in the herbarium of the University of Wisconsin, especially those of Dr. J. J. Davis and of Mr. L. S. Cheney, have been of great value. Specimens in the herbaria of the Milwaukee Public Museum and the Field Museum have been examined. Moreover, through the courtesy of Dr. O. C. Rosendahl, and Dr. J. H. Ehlers the herbaria of the Universities of Minnesota and Michigan have been referred to through correspondence. Acknowledgment for aid relative to the glacial geology is due Mr. F. T. Thwaites, who, together with many others, has offered suggestions and tendered information of great value. Particular acknowledgment is made for the generosity of Dr. Fassett in turning over the further investigation of the problem, and for helpful advice and criticism throughout the course of the work.

DEFINITION OF THE COASTAL PLAIN FLORA

The Coastal Plain as a physiographic province is clearly demarcated (Fig. 1). To quote from Bowman ('11), "The greater part of the eastern and southern coast of the United States is bordered by a lowland whose physiographic features are developed upon a mass of sands, silts, and clays, chiefly of Cretaceous and Tertiary age, and disposed in strata that incline gently seaward. . . . The Coastal Plain terminates on the north at Cape Cod, on the south in Mexico. Both ends are narrow, and the northern is glaciated and partly submerged. The physiographic features of the province are varied at two points by special features of the first order—the peninsula of Florida and the lower alluvial valley of the Mississippi. Its width varies from a fraction of a mile to 500 miles measured normal to the coast; its greatest inland development is in the Mississippi Valley where it swings northward into western Kentucky, southeastern Missouri, and eastern and southern Arkansas."

To the west of the Atlantic division of the province lies the Piedmont Plateau, differing from the Coastal Plain in its greater elevation and in being

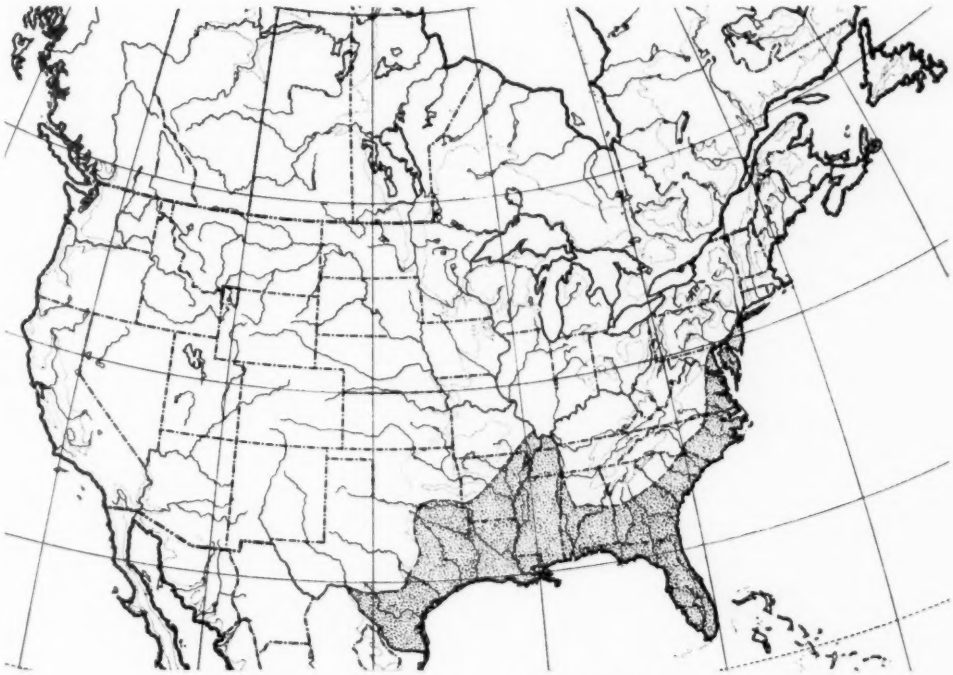


FIG. 1. The physiographic coastal plain.

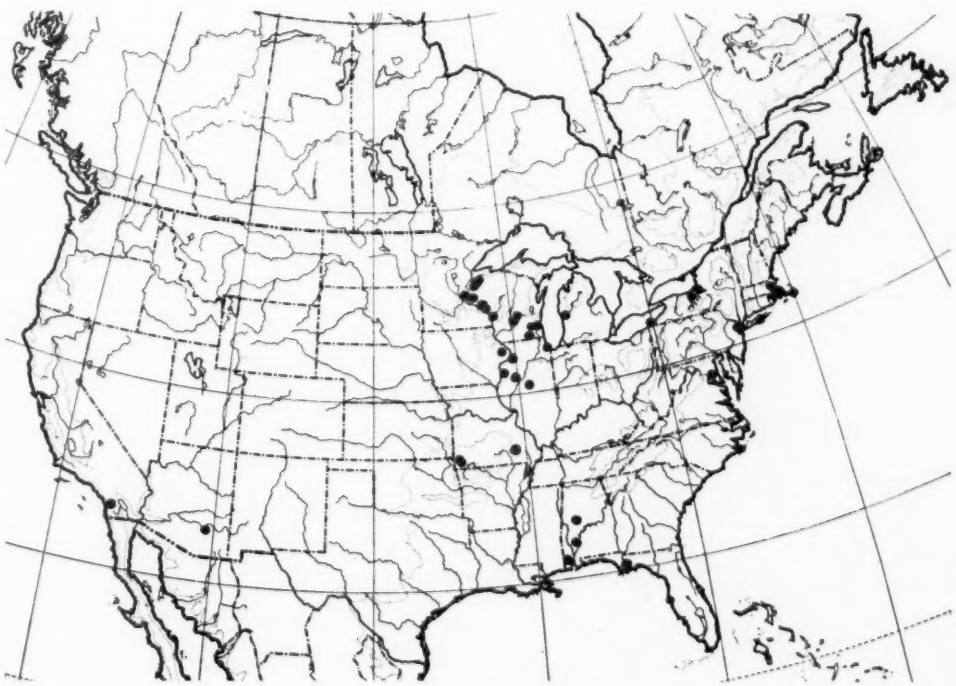


FIG. 2. Distribution of *Hemicarpha micrantha*.

formed upon crystalline rocks. According to Hitchcock and Standley ('19, p. 17) the floras of the two physiographic areas are noticeably different, though there are many species in common to the two regions. While the Coastal Plain may be thought of as a region of predominantly siliceous acid soil it must be realized that over so vast an area, extending through many degrees of latitude, soil and climatic conditions governing plant growth vary greatly. Even within a more circumscribed area considerable variation is to be expected. Thus within the coastal plain region of North Carolina Wells ('28) finds ten associations which he lists as dune, salt marsh, fresh water marsh, open water, swamp forest, pocosin or shrub bog, grass-sedge bog or "savannah," sand ridge, old field or meadow, and upland forest. Most of these associations could be projected into northwestern Wisconsin, excepting, of course, the salt marsh and swamp forest. Many of the species would be common to the two regions. These would include *Acorus Calamus, Pontederia cordata, Scirpus americanus, Zizania aquatica, Cyperus strigosus, Juncus canadensis, Rynchospora capitellata,* and *Castalia odorata.* However, the species extending to a greater or less degree over the Coastal Plain proper vary greatly in the extent of their range off the Coastal Plain, and in the relative frequency or rarity of their occurrence.

Some species of the Coastal Plain are definitely limited in their ranges to this region, and do not occur inland. Apparently *Fimbristylis puberula,* extending in the low flat sand barrens and salt marshes from the Carolinas, Florida, and Mississippi south to Argentina, finds inhospitable territory to the north and west. Quite otherwise is the range of a considerable number of species which, occurring on the coastal plain, also extend rather generally northward and westward. *Scirpus americanus,* also in Europe and South America, occurs on the borders of brackish and fresh water ponds and streams throughout temperate North America. *Hemicarpha micrantha,* chiefly on the Coastal Plain and in the flat country of the interior, on the sandy borders of ponds and streams, also extends west to New Mexico, Arizona, and California (Fig. 2). Again, *Eleocharis acicularis* on muddy shores, and *Typha latifolia* on marshy ground, extend across the continent, and are very much at home on the Coastal Plain. A third type of range is represented by such species as *Drosera rotundifolia* and *Sarracenia purpurea,* which, though occurring generally in boreal regions, also extend far south on the Coastal Plain where conditions favorable for their growth prevail. Thus *Rynchospora alba,* in bogs from Newfoundland to Alaska and Oregon, also extends south on the high mountains and in the Coastal Plain to Florida and west to Texas. Still another group of plants is represented by species which occur more or less generally throughout the Coastal Plain and extend inland only very locally and where conditions fulfill their rather specific ecological requirements. There appear to be two quite clearly marked arms of inland

FIG. 3. Distribution of *Betula nigra*.

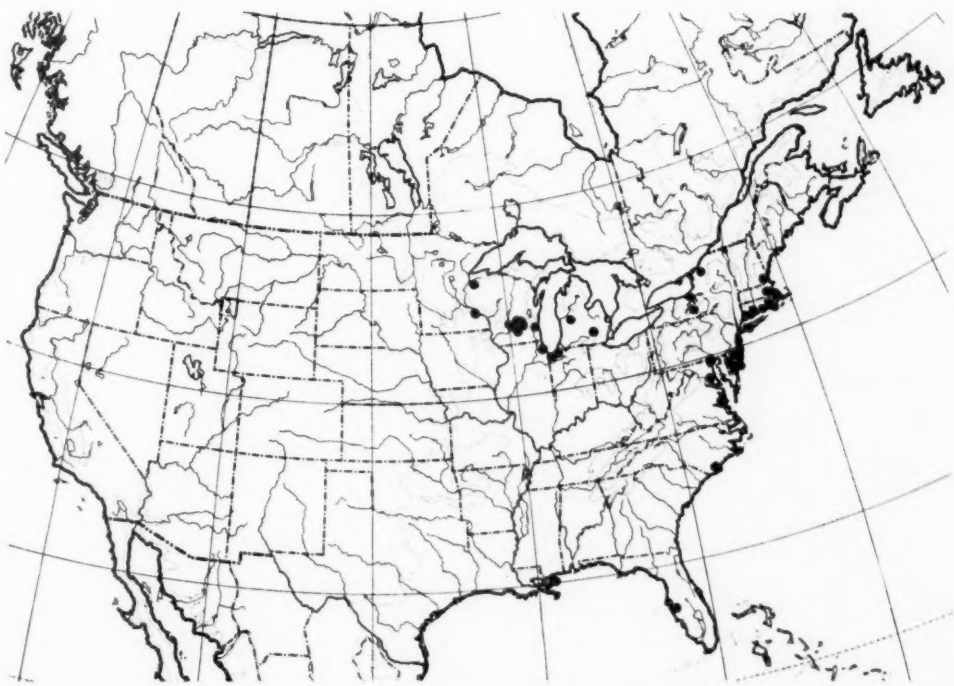


FIG. 4. Distribution of *Echinochloa Walteri*, including f. *laevigata*.

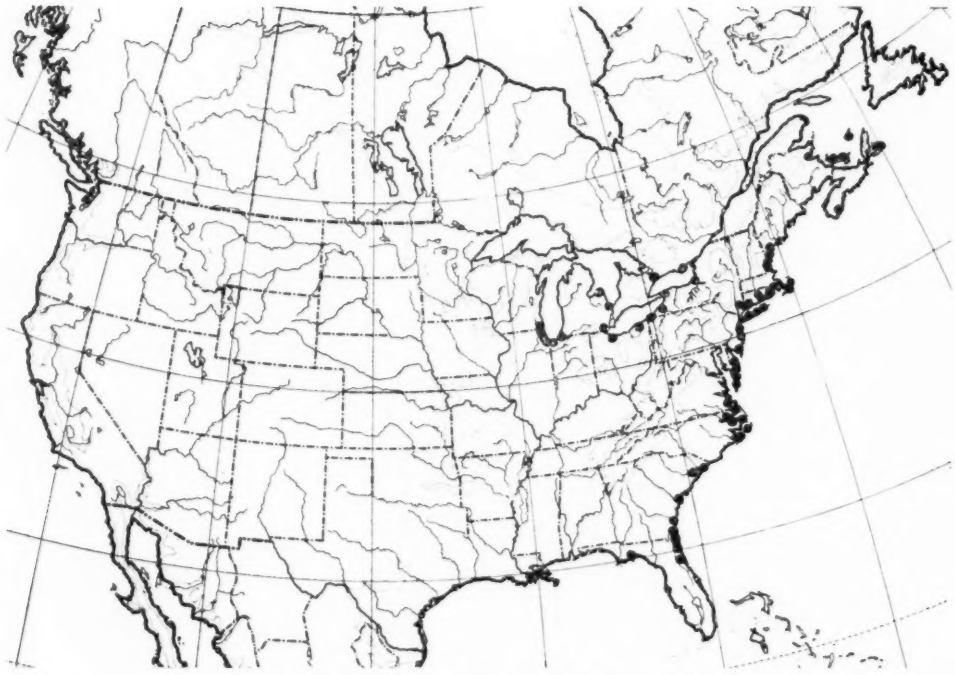


FIG. 5. Distribution of *Euphorbia polygonifolia*.

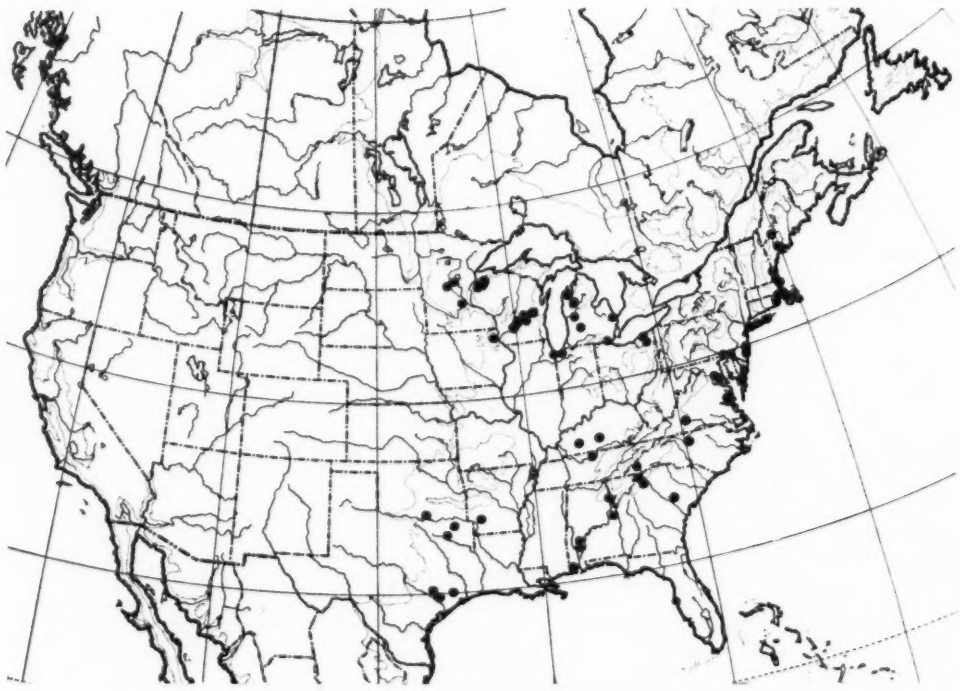


FIG. 6. Distribution of *Xyris torta*.

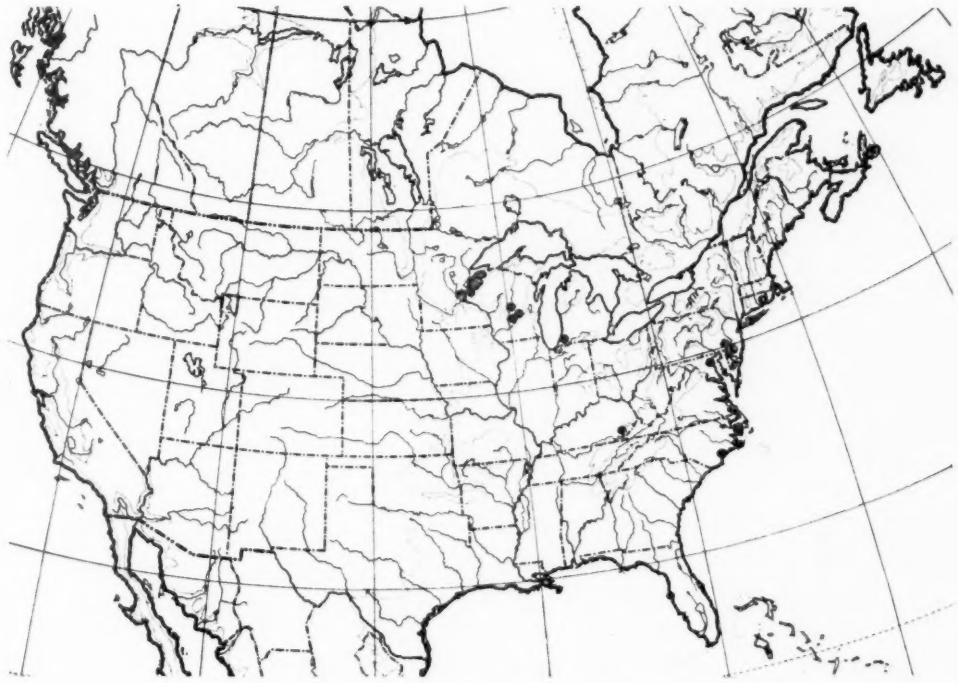


FIG. 7. Distribution of *Panicum albemarlense*.

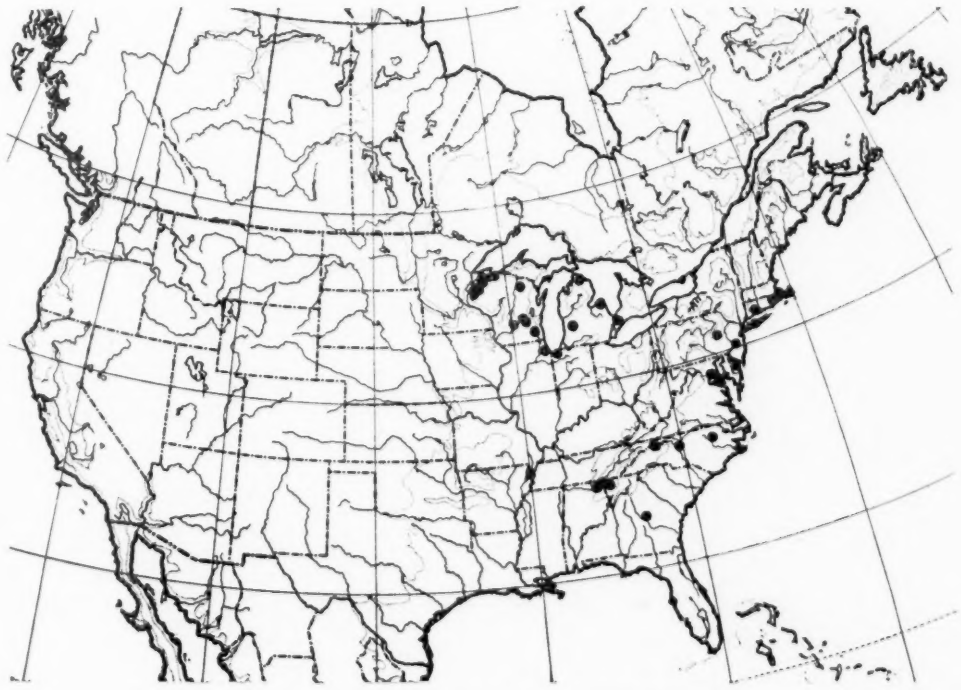


FIG. 8. Distribution of *Panicum meridionale*.

extension, the one up the Mississippi Valley as represented by the range of *Betula nigra* (Fig. 3), and the other about the Great Lakes. The latter range is represented by *Echinochloa Walteri* (Fig. 4) in swales, *Euphorbia polygonifolia* (Fig. 5), *Xyris torta* (Fig. 6), *Panicum albemarlense* (Fig. 7), and *P. meridionale* (Fig. 8) on sand shores. Finally a considerable number of species which occur within the sand barrens of northwestern Wisconsin appear to have an inland range about the Great Lakes similar to that of *Xyris torta*, and yet do not extend into the boreal regions nor far south on the Coastal Plain. Some of these, such as *Lycopodium inundatum* (also extending northward) and *Agalinis paupercula* and its var. *borealis* (Fig. 9), may be derivatives in more recent time of forms which do extend southward along the coast. In reference to the Lycopodium Harper ('05) writes, "In New England and elsewhere in the same latitudes *L. inundatum* is almost the sole representative of this group, but in the southern states are three species, all confined to the Coastal Plain." Pennell ('29) points out that *Agalinis purpurea* is almost alone among the *Purpureae* in occurring inland through the eastern United States far beyond the limits of the Coastal Plain. He considers that *A. paupercula* on lake shores and bogs may be a recent derivative of *A. purpurea* which has developed since the glacial retreat. He thus explains, "Perhaps we must consider *A. paupercula* to have been originally a species of the submerged Coastal Plain from which it has penetrated westward and northward, giving rise to two rather similar derivatives: *A. paupercula* var. *borealis* and *A. neoscotica* (of Nova Scotia and Sable Island)." However, in the case of *Muhlenbergia uniflora* (Fig. 10) the possibility of derivation from a related southern form is not so evident.

It would seem that these differences of inland extension are due to qualities inherent in the different plants, and are the result on the one hand of the degree of specificity of ecological requirements including temperature, moisture, sunlight, and soil conditions, and on the other hand of the method and effectiveness of seed dispersal. Both of these factors are of primary importance.

Thus in coming to a definition of the coastal plain flora one is faced with the very difficult question of where to draw the line, of how inclusive the definition should be made. Peattie ('22) rather arbitrarily delineated the coastal plain flora as the flora of the coastal plain region, of acid bogs, sand barrens, savannahs, and marshes, anywhere from the Gulf of Mexico and Florida to Cape Cod, Nova Scotia, and Newfoundland. He excludes the flora of the salt marshes and estuaries, and says, "nor does it include any of those plants which, though abundant upon the Coastal Plain, are found in a fairly general way in other areas, such as *Cenchrus carolinianus, Quercus ilicifolia, Strophostyles helvola, Tephrosia virginiana, Lespedeza capitata*, etc." However, *Echinochloa Walteri*, common in the east about fresh and

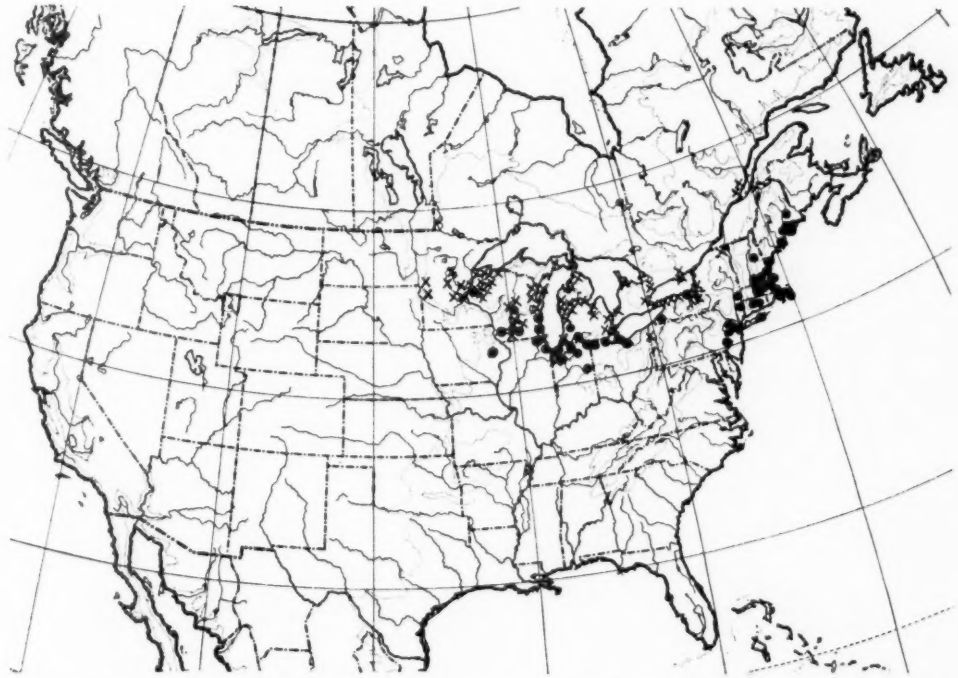


FIG. 9. Distribution of *Agalinis paupercula* (.), and var. *borealis* (x). Modified after Pennell.

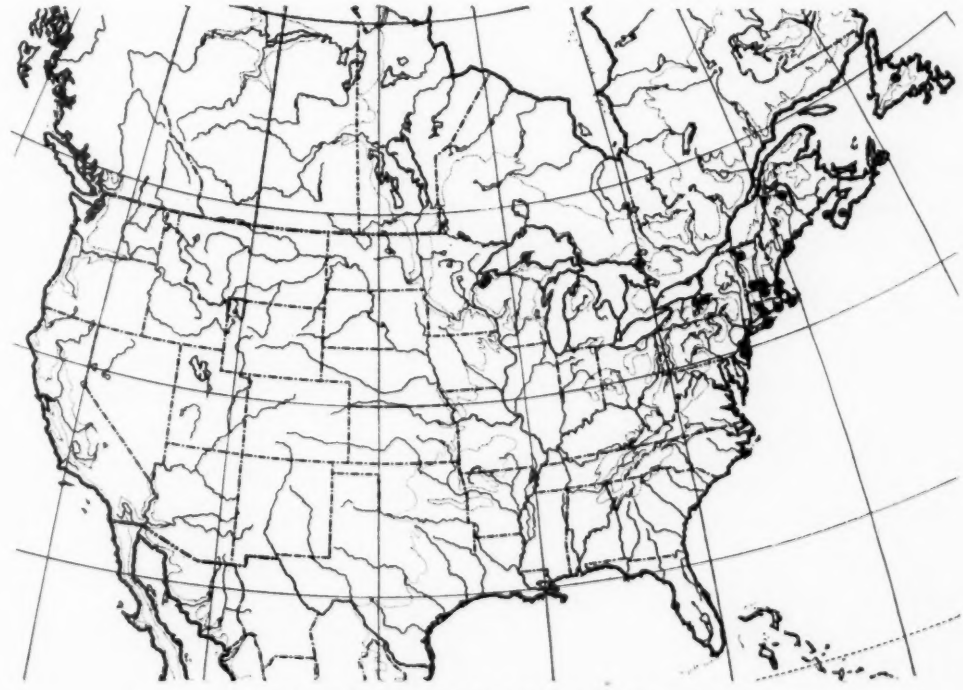


FIG. 10. Distribution of *Muhlenbergia uniflora*.

salt marshes, and *Elatine triandra* var. *americana* (*E. americana* of authors; see Fassett 1928a, p. 100; 1930b, p. 199; 1931, pp. 72-74.), typically an estuarine plant though occurring under non-estuarine conditions along the upper Ottawa River, are plants occurring inland under non-saline conditions, and with ranges comparable to plants of siliceous soils. It thus appears evident that in such cases, at least, salinity is not the governing factor.

The writer feels, in short, that an exact and exclusive definition of the coastal plain flora is not only impossible but quite unnecessary. Practically, however, the coastal plain flora as defined by Peattie, that is, essentially the group as outlined above which includes those species occurring on the Coastal Plain and extending inland with a limited range only, is the element with which the present paper is chiefly concerned.

Species Occurring in the Northwestern Wisconsin Sand Barrens, on the Atlantic Coastal Plain, and Extending Rather Generally Northward and Westward

This group includes a large number of species, some of which are generally limited in their inland ranges to areas of sandy soil; others are of common occurrence across the continent. The list does not pretend to be complete, but includes particularly those species which are more generally associated with the more conservative coastal plain types on the sandy shores of the northern lakes.

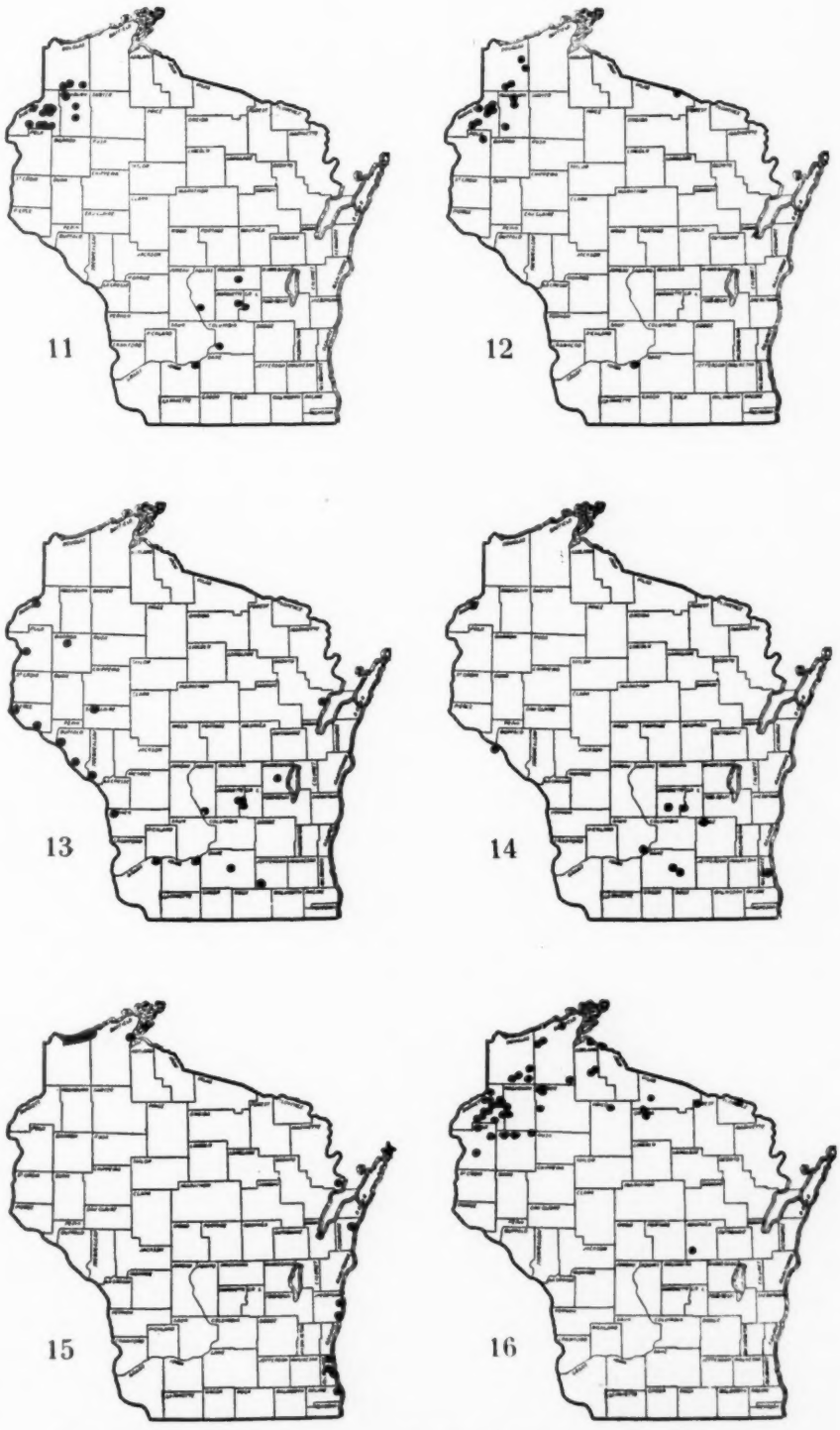
Sagittaria graminea, Calamagrostis canadensis, Leersia oryzoides Glyceria canadensis, Agrostis hyemalis, Cyperus diandrus (Fig. 13), *C. rivularis, C. aristatus, C. strigosus, Dulichium arundinaceum, Eleocharis acicularis, Scirpus debilis, S. americanus, Hemicarpha micrantha, Carex comosa, Acorus Calamus, Eriocaulon septangulare* With. (*E. articulatum* (Huds.) Morong of Gray 7th ed.), *Juncus balticus* var. *littoralis* (including f. *dissitiflorus* Engelm. See Fernald and Wiegand '10), *Calopogon pulchellus* (See map, Fernald '11a, pl. 89), *Spiranthes cernua, Myrica asplenifolia, Helianthemum Bicknellii* Fernald (*H. majus* of authors), *Viola lanceolata, Lycopus uniflorus, L. americanus, Linaria canadensis, Solidago graminifolia* (including var. *Nuttallii* (Greene) Fernald)[1], *Bidens connata* and varieties (Fig. 31 and accompanying discussion).

Species Primarily of Boreal Regions, Occurring within the Northwestern Wisconsin Sand Barrens, and Extending South on the Coastal Plain

These are, for the most part, plants of the sphagnum bogs which they are following from the glaciated area southward on the Coastal Plain.

Lycopodium inundatum (var. *Bigelovii* extends southward on the Coastal Plain to Maryland), *Rynchospora alba, Carex scoparia, C. Crawfordii, Juncus*

[1] Apparently this species has become somewhat weedy. Within Wisconsin there are several collections from the railroad right of way. In this connection Wiegand and Eames ('25, p. 402) remark, "The species has greatly increased in abundance in recent years."



FIGS. 11-16. Wisconsin ranges of (11) *Xyris torta;* (12) *Lycopodium inundatum;* (13) *Cyperus diandrus;* (14) *Echinochloa Walteri;* (15) *Lathyrus maritimus* (+) and var. *glaber* (.); (16) *Eriocaulon septangulare.*

brevicaudatus, J. canadensis, Ranunculus reptans (*R. Flammula* var. *reptans* of Gray 7th ed.), *Sarracenia purpurea, Drosera rotundifolia, Hypericum majus, H. virginicum, Cicuta bulbifera,* and *Vaccinium macrocarpon.*

Species Occurring more or less Generally Throughout the Coastal Plain, and Having only Limited Inland Extensions of Range which Include the Northwestern Wisconsin Sand Barrens

It is this group that includes the greater number of species listed by Peattie as coastal plain types.

Panicum albemarlense (Fig. 7), *Panicum meridionale* (Fig. 8), *Echinochloa Walteri* (Fassett '30a),[2] *Zizania aquatica* and vars. (including besides the typical form var. *interior* Fassett and var. *angustifolia* Hitchcock), *Aristida tuberculosa, Cyperus ferax, Fimbristylis autumnalis* (*F. Frankii* of Gray 7th ed.), *Rynchospora capitellata* (Michx.) Vahl. (*R. glomerata* (L.) Vahl. of Gray 7th ed. Includes var. *discutiens* Clarke), *Mariscus mariscoides* (Muhl.) Kuntze (*Cladium mariscoides* (Muhl.) Torr. of Gray 7th ed.), *Xyris torta* Sm. (*Xyris flexuosa* Muhl. of Gray 7th ed.), *Pontederia cordata* (includes f. *latifolia* and f. *angustifolia*), *Habenaria clavellata, Polygonella articulata, Spiraea tomentosa* var. *rosea,*[3] *Polygala cruciata, Helianthemum canadense, Utricularia gibba, U. resupinata* (Fig. 17), *U. cornuta* (Fig. 18), *Bidens discoidea,* and *Cirsium pumilum.*

Species with a Limited Inland Extension about the Great Lakes, Occurring in the Northwestern Wisconsin Sand Barrens, but Not Extending far to the Northward, nor Southward on the Coastal Plain

Muhlenbergia uniflora (*Sporobolus uniflorus* of some authors), *Scirpus Smithii, S. Torreyi, Juncus Greenei, J. pelocarpus, Agalinis paupercula* and var. *borealis* (Fig. 9).

The Effect of Physiographic Factors Upon the Distribution of Coastal Plain Plants in Wisconsin

A reference to the map (Fig. 11) illustrating the range of *Xyris torta* within Wisconsin makes evident the fact that there are two widely separated regions within which this coastal plain species occurs. In either case the areas are inland some distance from the Great Lakes. In Douglas, Washburn, and Burnett Counties the area concerned coincides approximately with the extensive sand barrens of northwestern Wisconsin (Fig. 19). In the south-central region the most outstanding fact is that two of the stations for this species are not in the drift covered area at all, but lie within the famous Driftless Area, a section of southwestern Wisconsin and adjacent Minnesota, Illinois and Iowa which was never covered by ice, although areas of glacial

[2] The report of a collection of this species from the Mississippi River bottoms, Grant County, Wisconsin has since been found to be based on a misdetermination.

[3] The interior form (Fernald '12) appears to be endemic to the region about the Great Lakes and to the southeastern mountains.

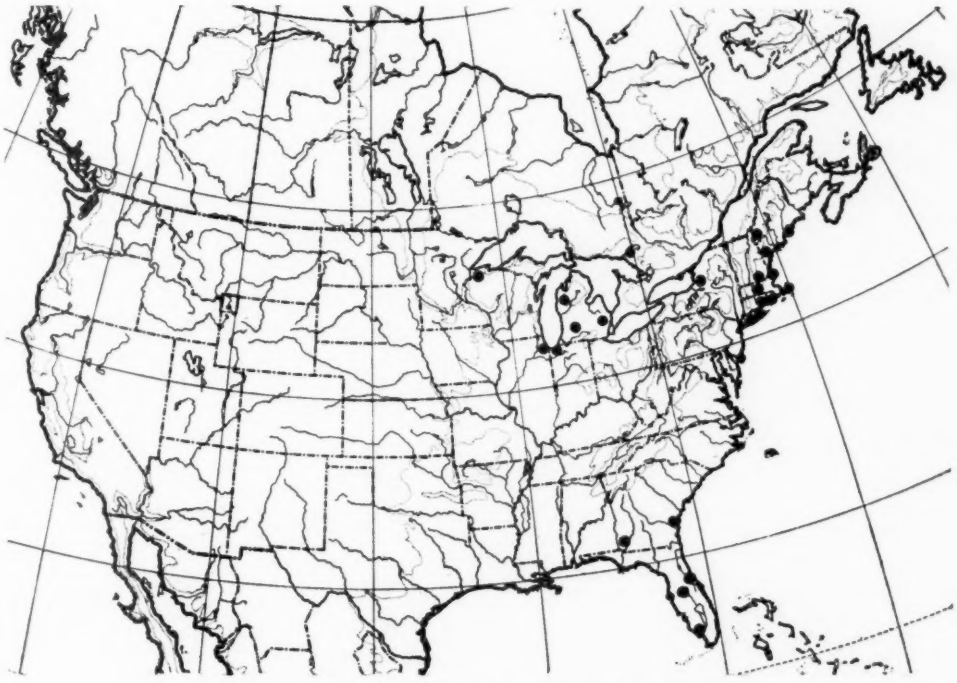


FIG. 17. Distribution of *Utricularia resupinata.*

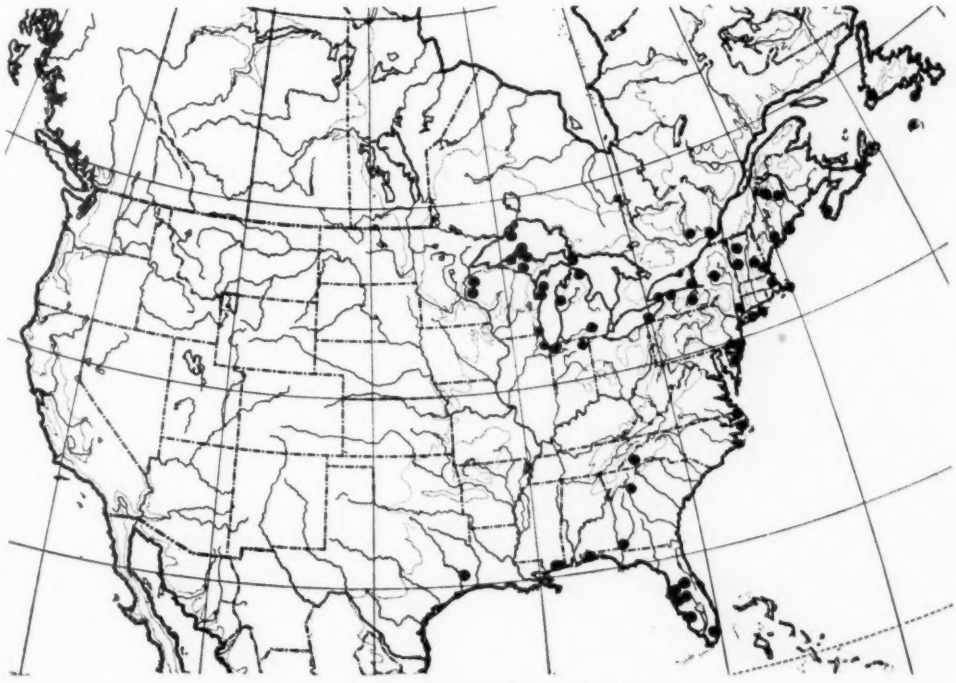


FIG. 18. Distribution of *Utricularia cornuta.*

drift extend on all sides and far to the southward. *Lycopodium inundatum* shows a similar restricted range (Fig. 12), but in addition to occurring in the northwestern sand barrens and in The Driftless Area at Arena, Iowa County, the species also appears in northeastern Wisconsin and in the Apostle Islands, Lake Superior.

Again, a considerable number of species, represented by *Cyperus diandrus* (Fig. 13) and *Echinochloa Walteri* (Fig. 14) range along the shore of Lake Michigan, into the south-central part of the state, apparently westward down the sandy bottoms of the Wisconsin River to the Mississippi, and thence northward up that river along the western margin of Wisconsin into the northwestern sand barrens.

A strikingly different range is represented by *Lathyrus maritimus* var. *glaber* (listed by Peattie as a coastal plain form), which is abundant along the Wisconsin shore of Lake Michigan and occurs on the Apostle Islands and rather generally along the Lake Superior shore, but is not known to have an inland station within the state (Fig. 15).

Finally a considerable number of species of coastal plain affinity are known within Wisconsin only from the northwestern sand barrens, or in the sand barrens and also further east in the northern part of the state. Such a range has *Eriocaulon septangulare*, with, however, verbal reports of two more southerly stations, one in Waupaca County, and one at Trempeleau on the Mississippi bottoms (Fig. 16). *Muhlenbergia uniflora* and *Utricularia resupinata* are of exceedingly rare occurrence, the former being known, within the state, from five, and the latter from one of the sandy-shored lakes in the northwestern sand barrens. Moreover, *Bidens connata* var. *pinnata* (Fig. 31), a variety originally described from Hennepin County, Minnesota, is now known to be endemic to northwestern Wisconsin and adjacent Minnesota.

Before one considers the possible explanation of the occurrence of coastal plain species within the northwestern sand barrens and elsewhere in the state a comprehension of some of the outstanding geological and physiographic features is of the utmost importance. Cambrian and post-Cambrian sedimentary rocks cover the southern part of the state except for occasional isolated pre-Cambrian knobs which project through from the crystalline base. Rising in a great flattened dome these dolomites, shales, and sandstones approach the high area of crystalline rocks to the north. On the extreme north, at the western end of Lake Superior, is the Lake Superior Lowland (Martin, '16, p. 401), underlain by the Lake Superior sandstone.

There are two great lake regions within the state, one in the northeastern and one in the northwestern part, although lakes occur in greater or less numbers throughout the glaciated area. Approximately 3,000 lakes and lakelets are shown on the various county maps (Juday and Birge, '30). The northeastern lake district is the highest part of the state, with elevations ex-

FIG. 19. The physiographic regions concerned in the migration of coastal plain plants into the northwestern Wisconsin barrens.

ceeding 1,800 feet. This area of high elevation continues eastward into Michigan to a point east of the Huron Mountains. The eastern portion of the Upper Michigan Peninsula, however, is at a much lower level and is a region of extensive marsh and sand plain. Botanically this region is still very imperfectly known.

The major part of the northwestern lake district lies within the sand barrens, a plain-like area heading near Iron River in Bayfield County, and sloping to the southwest at an average rate of about 3.0 feet per mile (Hansell, '30). Elevations range from about 1,160 feet on the northeast to about 860 feet on the north side of the St. Croix River. The St. Croix, flowing southwest into the Mississippi, approximates the western margin of the sand barrens over much of the distance (Fig. 19). Within the barrens are innumerable

lakes, some with marshy shores, many with wide, gently sloping sand beaches (Fig. 21). A large proportion of these lakes are in closed depressions, have no inlet or outlet, and are seldom of great depth.

Interspersed with the lakes are sphagnum bogs, some with open water in the center and others sufficiently dry so that the surface gives but little beneath the feet. Elsewhere the depressions are drier, and the sphagnum bog is replaced by flat open meadow (Fig. 23). Other lakes, such as Yellow Lake in western Burnett County have an inlet and outlet.

Perhaps the most striking characteristic of the sandy lakes is the series of well marked abandoned beaches, which, in many instances, extend in step-like succession to considerable elevations above the present water level. Accompanying the beaches are shorewise ridges, formed as bars and in some instances probably supplemented by ice-push. Upon the higher beaches dry lagoons extend along behind the bars, but the lowermost moist lagoons support a very characteristic coastal plain flora. Within the barrens the uplands are dry, sandy, flat or rolling plains which support, for the most part, a rather sparse stand of Jack Pine, oaks, poplars, etc. Further south, but still within the area formerly covered by the pro-glacial Barrens Lake, the soil changes abruptly to a calcareous clay, and this change is as strikingly reflected in the vegetation. Here the coastal plain flora, as occurring upon the acid sand beaches, is conspicuously absent.

The St. Croix River, draining the sand barrens, continues southward to join the Mississippi River a few miles southeast of St. Paul. The Mississippi gorge, extending for 200 miles along the western border of the state, varies in width from one to six and a half miles, and in depth from 230 to 650 feet. Within its floodplain this portion of the Mississippi descends to the south with a gradient of a little less than four inches to the mile (Martin, '16, p. 139). Sloughs, lakes, and islands abound. Aside from the floodplain the Mississippi bottoms contain a series of sand and gravel terraces which rise from 20 to a maximum of 235 feet above the present floodplain.

At Prairie du Chien, Crawford County, the Mississippi is met by the Wisconsin River, which, arising in the vicinity of Lac Vieux Desert on the Michigan-Wisconsin boundary, flows south to the vicinity of Portage, Columbia County, at which point the river abruptly turns southwest after skirting about the eastern end of the Baraboo Hills, and flows through a portion of The Driftless Area to the Mississippi. The lower course of the Wisconsin, within The Driftless Area, is through a valley filled with a terraced sand and gravel plain to a depth exceeding 150 feet in places. From these sand terraces and bottoms a considerable number of coastal plain species are known. The region near Arena, Iowa County, has yielded a particularly large number.

The Driftless Area in the southwestern corner of Wisconsin, in sharp contrast with the glaciated parts of the state, is characterized by a rough erosional

topography. Here are numerous sandstone crags, benches, and erosional escarpments. While The Driftless Area was never covered by ice, much of the present topography within this region is due to glaciation of the adjacent areas. Within the outwash plain and sandy pro-glacial lake bottom dunes have more recently developed. The Driftless Area as a possible haven for coastal plain species during the period of glaciation, and as a center from which post-Pleistocene migration might have occurred, is reserved for later discussion.

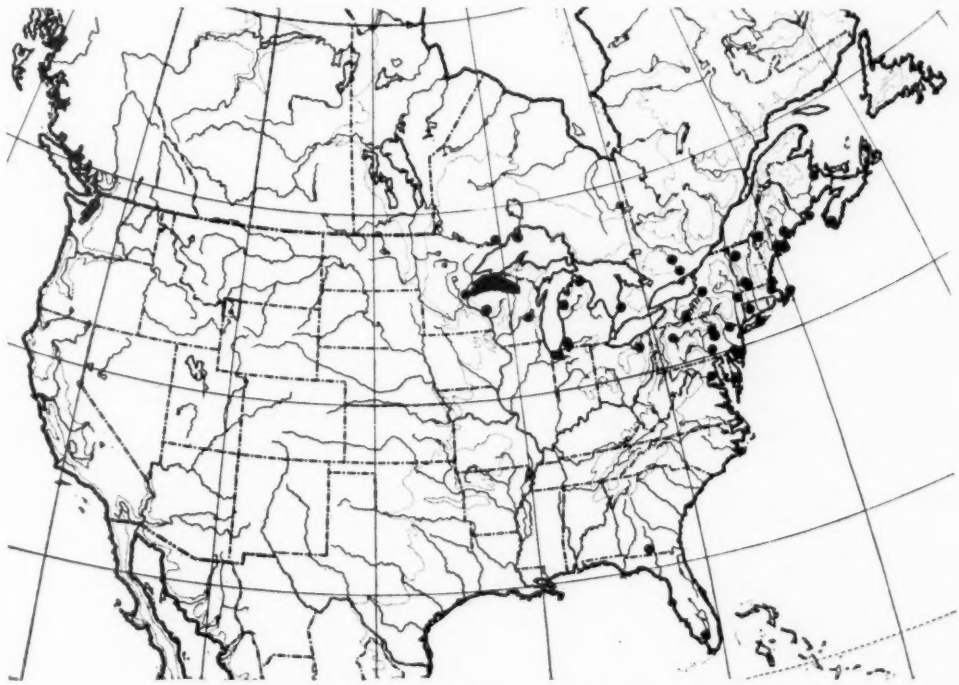


FIG. 20. The distribution of *Eriocaulon septangulare*.

In southeastern Wisconsin the Fox River Valley (Fig. 19) slopes northeast in a vale between the Niagara cuesta, forming the Door Peninsula on the east, and the Trenton cuesta on the west. The route of Marquette and Joliet was up the Fox River to its head near Portage, Columbia County, thence over the low marshy divide to the Wisconsin River, and southwestward to the Mississippi. In this region in the fall of 1929 such coastal plain types as *Bidens discoidea, Juncus Greenei,* and *Echinochloa Walteri* were found (Fassett, '30a). Many of the lakes of this region are distinctly of the "hard water" type with swale margins, and a luxuriant aquatic vegetation. Others, however, have the gently sloping sand beaches characteristic of the sandy-shored lakes of the northwestern barrens. Such a lake is Wingra south of Madison, Dane County, from which a considerable number of coastal plain species are known. Here is the only known station within the state for the coastal plain *Eleocharis interstincta.*

It now becomes apparent that there is an almost continuous line of lakes, swales, and sandy river bottoms extending across southern Wisconsin from Lake Michigan, westward down the Wisconsin River valley, and northward up the Mississippi bottoms to the northwestern sand barrens region. That conditions were at one time more favorable for the occurrence of the coastal plain element within these areas, and that this was indeed the pathway for the inland extension of many of these plants at a time probably coincident with the final retreat of the ice sheet from the region are the probabilities that have been brought out in this study.

It has been pointed out that Lake Superior, over much of its extent, at least, does not appear to offer hospitable conditions for the coastal plain element. The occurrence of *Lathyrus maritimus* var. *glaber, Rynchospora alba,* and a few other species, primarily of northern range, on the shores of Lake Superior is made the more striking by their total absence from within the northwestern sand barrens which are separated from the Superior Basin, only a few miles to the north, by an east-west ridge.

FIG. 21. The zonation of coastal plain plants on the sandy margin of Oak Lake, Burnett County, Wisconsin. The lake level was unusually low at the time when the photograph was taken (Sept. 10, 1930).

PLANT DISTRIBUTION AS RELATED TO GLACIATION

The Glacial Great Lakes

Peattie has clearly shown that the occurrence of coastal plain plants inland as at Presque Isle in Lake Erie, the Indiana sand dunes, the Ottawa

FIG. 22. Johnson Lake, Burnett County, Wisconsin. The foreground represents the beach of a former higher level of the lake. A sandbar (middle foreground) has cut off the sphagnum bog on the left from the open lake.

FIG. 23. Several species of *Carex* dominate the somewhat higher and drier part of the bog behind the sandbar at Johnson Lake.

FIG. 24. The swales at the margin of the open water at Johnson Lake include *Phragmites communis, Typha latifolia, Dulichium arundinaceum, Sagittaria latifolia, Eriocaulon septangulare,* and *Carex comosa.* The floating, "islands" are *Pontederia cordata.*

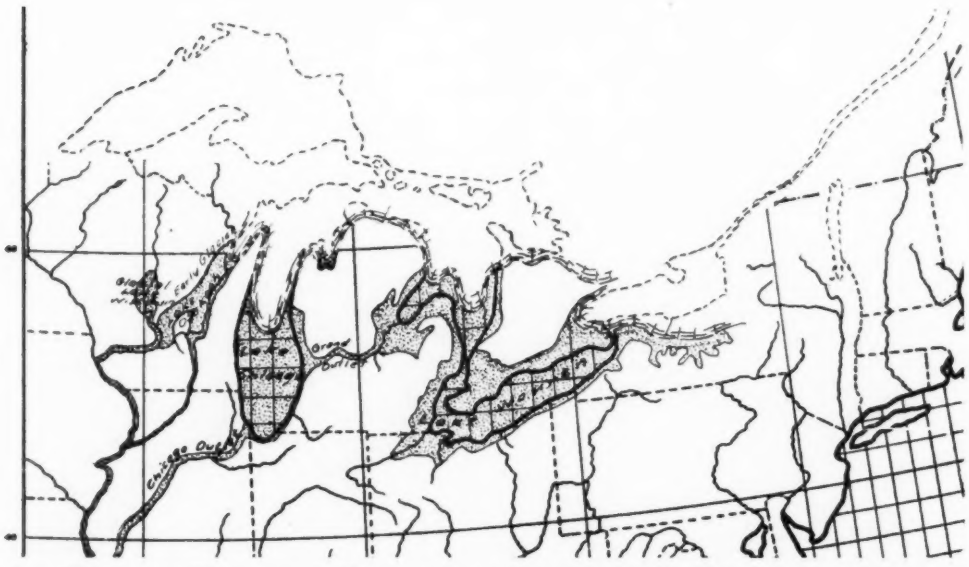


FIG. 25. Lakes Chicago and Warren stage of the Glacial Great Lakes. Lake Chicago drains through the Chicago Outlet. Presumably the Grand River connective was functioning at about this stage. The northeastward retreat of the Green Bay lobe, which at its greatest extent functioned as a dam to form Glacial Lake Wisconsin, has left Early Glacial Lake Oshkosh in the Fox River Valley.

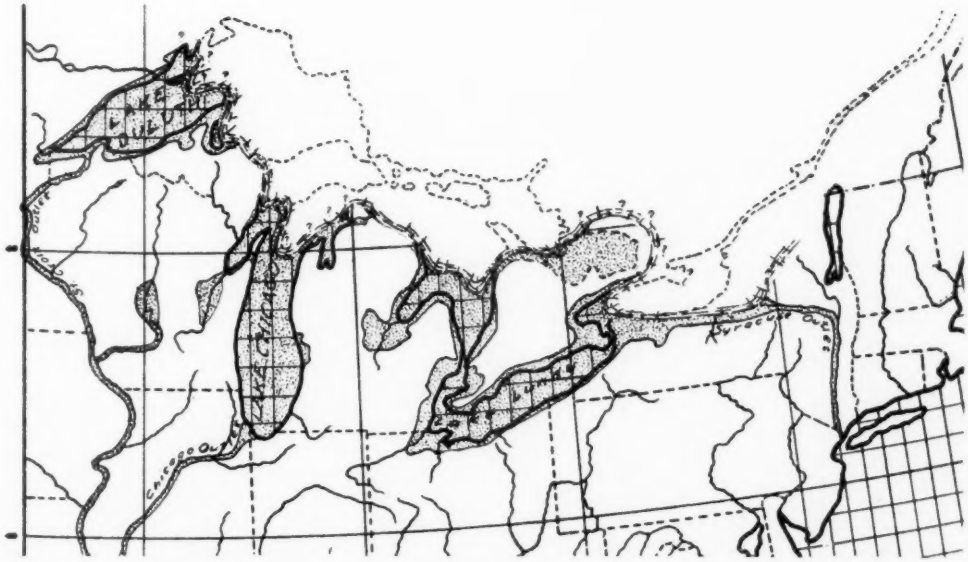


FIG. 26. Lakes Chicago and Lundy stage. The Glacial Great Lakes are in part draining eastward through the Syracuse Outlet. The further retreat of the ice has opened Glacial Lake Duluth in the Superior Basin. Figs. modified after Taylor and Leverett.

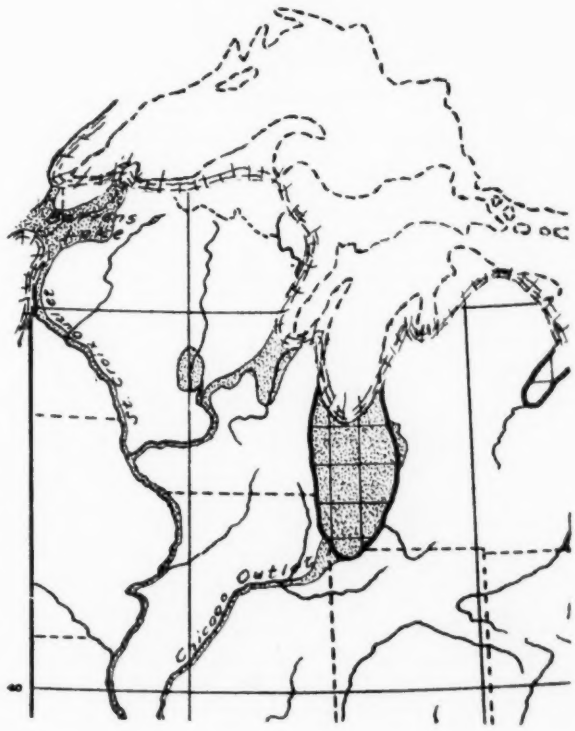


FIG. 27. A hypothetical correlation between the "Red Ice" readvance in the Fox River Valley and the northeastward advance of the Grantsburg Lobe damming up the waters of Barrens Lake in northwestern Wisconsin. The opinions of geologists regarding this correlation are at variance.

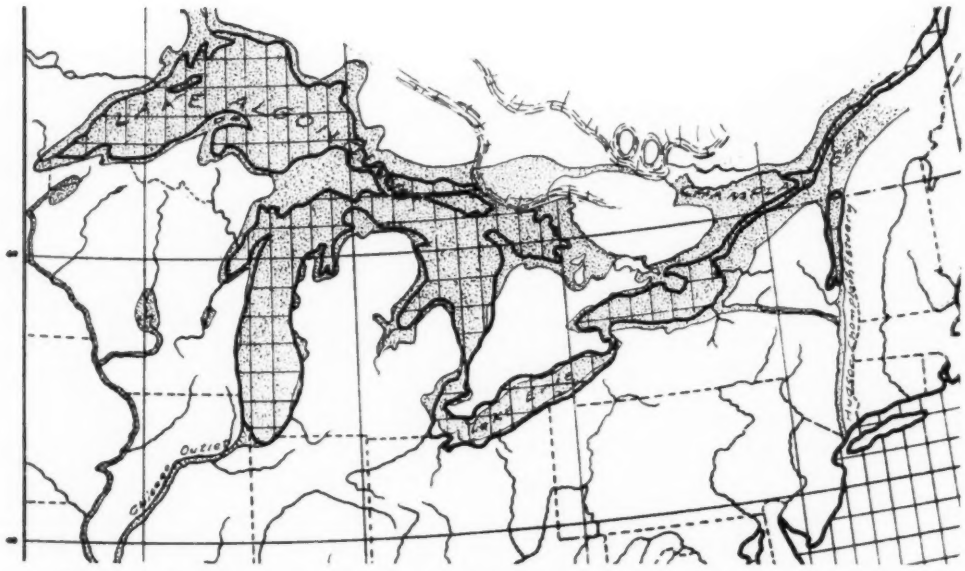


FIG. 28. Glacial Lake Algonquin and its correlatives. Modified after Taylor and Leverett.

River Valley, the Mohawk Valley, and the Finger Lakes of New York, as well as elsewhere adjacent to the Great Lakes, is directly related to the glacial history of the Great Lakes. He starts with the assumption that the recession of the last ice advance left the Great Lakes region open to occupancy by vegetation, and among the immigrating floras was that of the coastal plain. He suggests that at the time when the ice was receding the sand barrens, swales, and lagoons resulting from glaciation were far more extensive than at present. Thus he explains, "Judging from the large number of old spits and beach ridges which have been traced out for the glacial lakes giving rise to Lake Erie and Lake Michigan, it is reasonable to imagine their shores to have been an intricate series of lagoons, ridges, strands, and low dunes, harboring the newly migrated coastal plain and strand types."

According to Taylor ('12), during the Lakes Chicago and Warren Stage (Fig. 25) of the glacial Great Lakes there existed a connective across the Grand River Valley of southern Michigan. Lake Chicago was draining southwestward through the Chicago outlet. Lake Warren, in the Erie Basin, extended eastward into the Finger Lakes district of New York. At the Lakes Chicago and Lundy Stage (Fig. 26) the ice had withdrawn in part from the western end of the Superior Basin leaving Glacial Lake Duluth with an outlet through the Brule and St. Croix Rivers. Lake Chicago continued to drain through the Chicago outlet, but the Grand River connective had ceased to function, and Lake Lundy in the Erie Basin had found an outlet eastward past the ice margin down the Mohawk and Hudson River Valleys. From the present flora of the Ottawa River Valley, the Hudson and Mohawk Valleys,

and the Grand River Valley, Peattie finds evidence that these connectives were formerly paths of westward migration for coastal plain species. Thus from the Hudson-Mohawk Valley and the Finger Lakes of New York he lists *Woodwardia virginica, Hemicarpha micrantha, Echinochloa Walteri, Scirpus Smithii, Juncus balticus* var. *littoralis, Lathyrus maritimus* var. *glaber* and many others. It would seem, however, that if the Hudson-Mohawk and the Grand River connectives were pathways for the westward migration of these plants, it is necessary to also take the corollary view that the Grand River connective must have continued to function for some time after the opening of the Hudson-Mohawk outlet.

Two other possible routes of inland migration should be mentioned. According to Taylor, during the later stage of Lake Algonquin (Fig. 28) there was a connective through what is now the French River Valley of Ontario to Lake Nipissing, thence over the low-lying area east of Lake Nipissing to the Mattawa and the Ottawa Rivers. To Peattie's list of species from the Ottawa Valley of *Juncus pelocarpus, Utricularia resupinata, Elatine americana, Carex exilis, Muhlenbergia uniflora,* and *Isoetes riparia* might be added *Lathyrus maritimus* var. *glaber* from Lake Nipissing. Of these species, however, all but the *Juncus* and the *Utricularia* are of northern range and do not extend far south on the Coastal Plain. It will be observed (Fig. 28) that it was presumably during the later stages of Lake Algonquin that this connective between that part of Glacial Lake Algonquin which lay in the Lake Huron Basin and the Champlain Sea in the St. Lawrence-Ottawa Valleys was finally opened by the continued recession of the ice sheet to the north. Apparently then, the pathway for the inland migration of the coastal plain flora would have been open much sooner in the Hudson-Mohawk Valley, and these species which occur in the Ottawa Valley at present are those which had extended further northward. The occurrence of *Utricularia resupinata* within the Mohawk Valley and in the Grand River Valley of Michigan (Fig. 17) would seem to indicate an early inland extension of the species at the time (Lakes Chicago and Lundy stage?) when the Grand River connective was still functioning. The occurrence of this species also in the Ottawa River Valley would appear to indicate that it had followed the retreating ice front northward, and later migrated up the Ottawa connective. It is significant that the number of coastal plain types known from this latter region is not large, and suggests that the considerable number (Fernald, '11a, p. 139) which occurs in Newfoundland and Nova Scotia must have migrated northward over the now submerged coastal shelf at a somewhat later time, when the Ottawa connective was no longer functioning.

Peattie concludes that few, if any, of the coastal plain plants of the Great Lakes region have come northward up the Mississippi Basin and cites *Betula nigra* as having a northern range on the Kankakee River in northeastern Illi-

nois in support of this statement. However, the northern limit for this species (Fig. 3) is in the vicinity of the Twin Cities in the Mississippi bottoms, and likewise far to the northward up the Wisconsin River (Fassett, '30, p. 191). Moreover, *Hemicarpha micrantha* (Fig. 2) certainly extends up the Mississippi Basin, although it also occurs about the Great Lakes and inland in New York state. *Nelumbo lutea* has a similar range.

It appears to be the case, then, that the region about the Indiana dunes may have received coastal plain species from two and possibly three different sources: from the Mississippi Basin, from the Mohawk-Hudson outlet and the eastern Great Lakes, and from the Ottawa connective. It therefore appears entirely reasonable that there should be, as is the fact, a larger number of coastal plain species at this meeting place with its favorable ecological conditions preserved than at any other known station inland. It appears furthermore, that this region, as a gathering point, was the center from which the greater number of coastal plain species migrated northward along the Wisconsin shore of Lake Michigan, westward and southwestward down the Fox River Valley, down the sandy bottoms of the Wisconsin River to the Mississippi, and thence northward to the region of the northwestern Wisconsin sand barrens.[4]

Glaciation as Related to the Extension of Coastal Plain Plants into Wisconsin

Wisconsin, previous to the last or Wisconsin stage of glaciation, was probably covered by glacial ice at least three times. The Driftless Area in the southwestern part of the state, due to a combination of circumstances, remained free of ice. Although glacial drift entirely encircles the region it is probable that ice never completely isolated The Driftless Area at any one time.

The periods of ice advance were separated by interglacial intervals during which the ice withdrew, the climate was ameliorated, and vegetation undoubtedly abounded. Although plants of the Atlantic Coastal Plain may have been present within the central United States and inside the glaciated areas during the earlier interglacial intervals, these plants, excepting possibly within The Driftless Area or in similar unglaciated, isolated localities, must surely have perished upon the last return of the continental glaciers. This last or Wisconsin stage was not a single advance and retreat, but was characterized by an oscillation of the ice front, by several minor advances and retrogressions, presumably depending upon climatic factors. It is particularly significant that during at least one of these periods when the ice had retreated somewhat to the northward the climate was sufficiently mild for the growth of plants within the Fox River Valley (Lawson, '02), and at Two Creeks, Manitowoc County, along the Lake Michigan shore. It seems quite certain, there-

[4] The entire question of the migration of plants as related to continuity of suitable habitat has been competently discussed by Gleason (p. 48, 1922).

fore, that there were even trees of considerable size, as is evident at the Two Creeks forest bed, before the ice had withdrawn for the last time, for here the forest bed is covered by the red till which gives the name of "Red Ice" to the last stage of the ice advance within this region.

A reference to the map (Fig. 25) will make clear the fact that during the Lakes Chicago and Warren Stage of the Great Lakes there existed a large ice lobe in the Lake Michigan Basin, and another, separated from the Lake Michigan lobe by the eminence of the Door Peninsula, lay within the Fox River Valley in Wisconsin. Previous to the phase pictured in this figure the Michigan lobe had extended further south, completely filling the basin, and the Green Bay lobe in the Fox River Valley had extended southwest to a point in the vicinity of Portage, Columbia County. Here the ice, abutting against the quartzite Baraboo Hills, formed a dam which impounded the glacial waters to form an extensive lake, Glacial Lake Wisconsin, within The Driftless Area. Now, as the Green Bay lobe receded northeastward up the Fox River Valley, an outlet for Glacial Lake Wisconsin was opened around the east end of the Baraboo Hills, and thus the present course of the Wisconsin River was established. Moreover, as the ice retreated it formed another marginal lake within the Fox River Valley which has been termed Early Glacial Lake Oshkosh (Thwaites, '27b). If the stages of the Great Lakes as given by Taylor ('12, see maps) are essentially correct, there was no outlet at this time yet opened down the Hudson-Mohawk Valleys. Thus any coastal plain plants growing within the region at the head of Lake Chicago would necessarily have come in from the southern Coastal Plain up the Mississippi Basin. The comparatively few plants of coastal plain origin at present extending up the Mississippi Basin suggest that it was, therefore, at a later stage that the inland migration occurred.

The continued recession of the ice front was, as we have seen, marked by the formation of Glacial Lake Duluth in the Superior Basin (Fig. 26), and by the opening of the Hudson-Mohawk connective. At this time there still remained a lake of considerable extent in south-central Wisconsin (Postglacial Lake Wisconsin), and also a lake in the Fox River Valley centering about the basin of the present Lake Winnebago. Apparently the ice continued to retreat to a point beyond the Straights of Mackinac (Alden, '18, p. 315). It was, presumably, during this interval, while the ice was retreating northward and before the readvance, that the forest developed at Two Creeks, Manitowoc County. It may be, moreover, that it was at this time that certain of the coastal plain plants which may, by this time, have become established in the Chicago region, migrated northward along the marginal beaches in swales and sandy lagoons, and then, following the Fox River Valley and the lake margins, have continued on southwestward. The exact time of this migration must remain, for the present at least, an unsettled question. The

glacial history of the Great Lakes is still very imperfectly known, and the presence of peat deposits below the level of Lake Michigan (Alden, '18, p. 334) suggests a possible lower level of Lake Chicago, and a high degree of complexity regarding possible sub-stages of the glacial lakes.

Then conditions changed. Perhaps there was a lowering of the temperature. Once again the ice advanced (Fig. 27). At this time, however, the ice in the Michigan Basin never extended south to fill the entire basin and Lake Chicago remained at about the same level. The Green Bay lobe, advancing down the Fox River Valley, again formed a glacial lake, later Glacial Lake Oshkosh, which drained westward through a channel over the present low divide between the Fox and Wisconsin Rivers.

Whether the plants migrated into the Fox River Valley before or after this last advance of the ice appears to be of no great significance. Down the sand bottoms of the Wisconsin River Valley conditions favored their growth and the pathway was open to the Mississippi. Among those species which might be considered as being of coastal plain relationship and which survive to the present time at Arena, Iowa County, on the sand terraces and bottoms of the Wisconsin River are *Aristida tuberculosa, Fimbristylis autumnalis, Hemicarpha micrantha, Polygonella articulata, Lupinus perennis* var. *occidentalis, Polygala cruciata, Rotala ramosior, Agalinis paupercula, Linaria canadensis, Rynchospora capitellata, Stenophyllus capillaris, Xyris torta,* and *Rhexia virginica.* The range of the *Rhexia,* however, is more likely explained as having extended from the southern Coastal Plain up the Mississippi Basin. It does not extend north up the Mississippi to the region of the sand barrens.

The Glacial and Post-Glacial History of the Upper Mississippi as Related to the Northward Migration of Coastal Plain Plants

The coastal plain species which occur at present within the Mississippi bottoms along the western margin of Wisconsin include *Aristida tuberculosa, Fimbristylis autumnalis, Hemicarpha micrantha, Polygonella articulata, Nelumbo lutea, Panicum meridionale, Bidens discoidea, Juncus Greenei, Betula nigra,* and *Pontederia cordata* f. *latifolia. Eriocaulon septangulare* is reported from Trempeleau County by Mr. F. M. Uhler, but is not represented from the Mississippi bottoms by collections in the herbarium of the University of Wisconsin. It remains a fact, however, that many species present in the Fox River Valley and in the northwestern barrens are absent from the Mississippi bottoms at present. These include *Panicum albemarlense, Scirpus Smithii, Juncus balticus* var. *littoralis, Polygala cruciata, Agalinis paupercula* and var. *borealis. Utricularia gibba* is not known from the Fox River Valley, but occurs at the Dells of the Wisconsin River in Adams County within the former bed of Glacial Lake Wisconsin, at Lake Wingra near Madison, and in a floating bog west of Holcombe, Chippewa County. This diminutive bladderwort

is also known from the sandy shore of Oak Lake, Burnett County. Other species present in south-central Wisconsin and on the lakes of the sand barrens, but absent from the Mississippi bottoms are *Xyris torta*, *Rynchospora capitellata*, and *Lycopodium inundatum*.

If the Mississippi bottoms were the pathway northward for many coastal plain plants why are so many absent from the region today? The probable answer lies in the post-Pleistocene history of the river. The more recent history of the Mississippi bottoms (Martin, '16, p. 166) began with the deposition of sand and gravel, laid down as outwash by water flowing from the ice sheet. In places this filling is more than 250 feet. Conditions then changed, and instead of deposition there was erosion and cutting which resulted in the formation of the terraces. This may have been due to the retreat of the ice sheet to the northward, to tilting of the land surface, or to large volumes of comparatively sand-free water from glacial lakes. More recently there has been another change, and the Mississippi is depositing a floodplain of fine clay and silt. It is, therefore, evident that ecological conditions have changed within the bottoms since the time when the coastal plain plants migrated northward. It is presumably those species only which are more tolerant of silts and clays, of those which are able to exist on the dry sand terraces that have remained to the present day.

The Superior Basin as a Possible Pathway for the Extension of Coastal Plain Plants into the Sand Barren

Two facts of special significance stand out in regard to the flora of the Superior Basin; the one is the decided northern affinity of the greater number of species; the other is the total absence of so many coastal plain types that are present in the northwestern sand barrens from the Superior shore, and conversely the presence of a number of forms on Lake Superior which appear to be wholly absent from the sand barrens. The following species, present in the sand barrens, are not known from Lake Superior: *Panicum albemarlense*, *P. meridionale*, *Echinochloa Walteri*, *Fimbristylis autumnalis*, *Scirpus Smithii*, *Hemicarpha micrantha*, *Juncus pelocarpus*, *Polygala cruciata*, *Agalinis paupercula*, *Utricularia gibba*, *U. resupinata*, *Bidens discoidea*, *B. connata* var. *pinnata*, *Mariscus mariscoides*, and *Rynchospora capitellata*.

Those species present on Lake Superior, but absent from the sand barrens include *Ammophila breviligulata*, *Rynchospora alba*, and *Lathyrus maritimus* var. *glaber*. Species in common to the two regions are largely those which are of more general distribution wherever conditions suitable for their growth occur, and include *Drosera rotundifolia*, *Dulichium arundinaceum*, *Eleocharis acicularis*, *Elymus robustus* var. *vestitus*, *Glyceria canadensis*, *Hudsonia tomentosa* var. *intermedia*, *Juncus brevicaudatus*, *Vaccinium macrocarpon*, *Carex scoparia*, and *C. Crawfordii*. It will thus be seen that the coastal plain flora

of the Barrens Lake region is far more closely related to that of the Fox and Wisconsin River Valleys of southern Wisconsin than it is to the flora of Lake Superior. This seems more reasonable when it is considered, as has been pointed out by Peattie ('22, p. 85), that Lake Superior was the last of the Great Lakes to be uncovered by the ice, and that migration of coastal plain plants into southern Wisconsin may have occurred at a time previous to the opening of a route northward from the basin of Lake Michigan into that of Lake Superior.

There is some evidence, however, in support of the possibility that some of these species may have migrated from the Superior Basin into the Barrens Lake region. There are a number of plants of coastal plain range, some among them with a limited inland extension, which are common to the two regions. Thus *Pontederia cordata* is of general occurrence in lakes within the northwestern barrens, and is present *(f. angustifolia)* on the Superior shore of Ashland County. *Utricularia cornuta,* with a few stations within the barrens, is also present on the Door Peninsula, in the extreme eastern end of the Upper Michigan Peninsula, and in Lake Superior on Isle Royale and at several stations along the Bayfield and Ashland Counties Shore (Fig. 18). Moreover, *Muhlenbergia uniflora* (Fig. 10), *Eriocaulon septangulare* (Fig. 20), and *Solidago graminifolia* occur within the barrens, at various points on the shore of Lake Superior, and are also known from the Ottawa River Valley. Might, then, these plants have migrated at a somewhat later time, upon the opening of the Ottawa connective (Fig. 28), into the Superior Basin, and thence into the region of Barrens Lake?

It has been pointed out that conditions are not, for the most part, such as to be favorable to the occurrence of coastal plain species along the Superior shore. Although there are many places, as the extreme northern point of Ashland County, which are low, much of the shore is bordered by extremely precipitous bluffs with no sand beaches, or with merely locally developed beaches and points. However, the recent discovery (Wilson, '31) of peat deposits covered by sand considerably below the present level of Lake Superior may be of considerable significance in regard to the explanation of the migration of the coastal plain plants. Just as conditions have changed within the Mississippi bottoms since the migration of the coastal plain plants there, so may the raising of the level of Lake Superior have eliminated the habitat of some of the plants by submergence of the sand beaches.

The Pro-Glacial Barrens Lake as Related to the Distribution of Coastal Plain Plants within the Region

We have seen that in the Fox River Valley the retreat of the Middle Wisconsin Ice Sheet left Early Glacial Lake Oshkosh as an extensive pro-glacial lake (Fig. 25). At the same time the Lake Michigan lobe of the

glacier, on retreating, left Glacial Lake Chicago in the lower part of the basin. Presumably the simultaneous withdrawal of the ice from the Superior Basin left Glacial Lake Duluth. When the ice advanced for the last time (contemporaneously with the advance of the Last Wisconsin or "Red Ice" which buried the forest bed at Two Creeks, Manitowoc County?) there appears to have been a lobe in northwestern Wisconsin and adjacent Minnesota which advanced northeastward up the trough of the present sand barrens (Hansell '30), and, blocking the drainage, formed a lake (Fig. 27). This was the large lake which extended over much of the barrens of northwestern Wisconsin, and of which the present lakes are merely small relics. Now, as the ice retreated again to the southwest, the level of the lake fell as new and lower outlets were opened, but there remained a somewhat smaller body of water within the region until a later time when the outlet was eroded and the lake finally drained. There still remained numerous kettle depressions within the bed of the larger lake, and these, retaining water, have remained in many instances to the present day as lakes. We may picture, then, the coastal plain plants, migrating northward up the sandy bottoms and slough margins of the upper Mississippi River, establishing themselves upon the margin of the large Barrens Lake, and, as the lake margin receded, following the water margins until they had become isolated upon the present lake shores. At one time there were undoubtedly many more lakes within the region than exist there at present, as is suggested by the numerous and extensive bogs, and by many dry depressions where the coastal plain plants can, for the most part, no longer find favorable ecological conditions and so have perished.

A reference to the maps showing ranges of the more highly specific and conservative coastal plain species will serve to indicate that there is a striking agreement between the ranges of these plants in northwestern Wisconsin and the limits of the Barrens Lake as worked out upon purely geological evidence (Hansell '30). As a summary of this relationship 21 such species are mapped (Fig. 29) as they occur within the bed of the former Barrens Lake, and in adjacent areas. These plants are as follows: *Lycopodium inundatum, Panicum albemarlense, P. meridionale, Echinochloa Walteri, Muhlenbergia uniflora, Scirpus Smithii, Hemicarpha micrantha, Fimbristylis autumnalis, Eriocaulon septangulare, Pontederia cordata, Xyris torta, Juncus balticus* var. *littoralis, J. pelocarpus, Elatine minima, Utricularia cornuta, U. gibba, U. resupinata, Polygala cruciata, Bidens connata* var. *pinnata, B. discoidea,* and *Mariscus mariscoides.* There is no attempt made here to differentiate among the different species in the mapping, but merely to indicate the relative number of species from the above group which occurs upon the shores of the different lakes.

It is evident that the lakes of eastern Burnett, western Washburn, and southeastern Douglas Counties are those that have the greatest number of

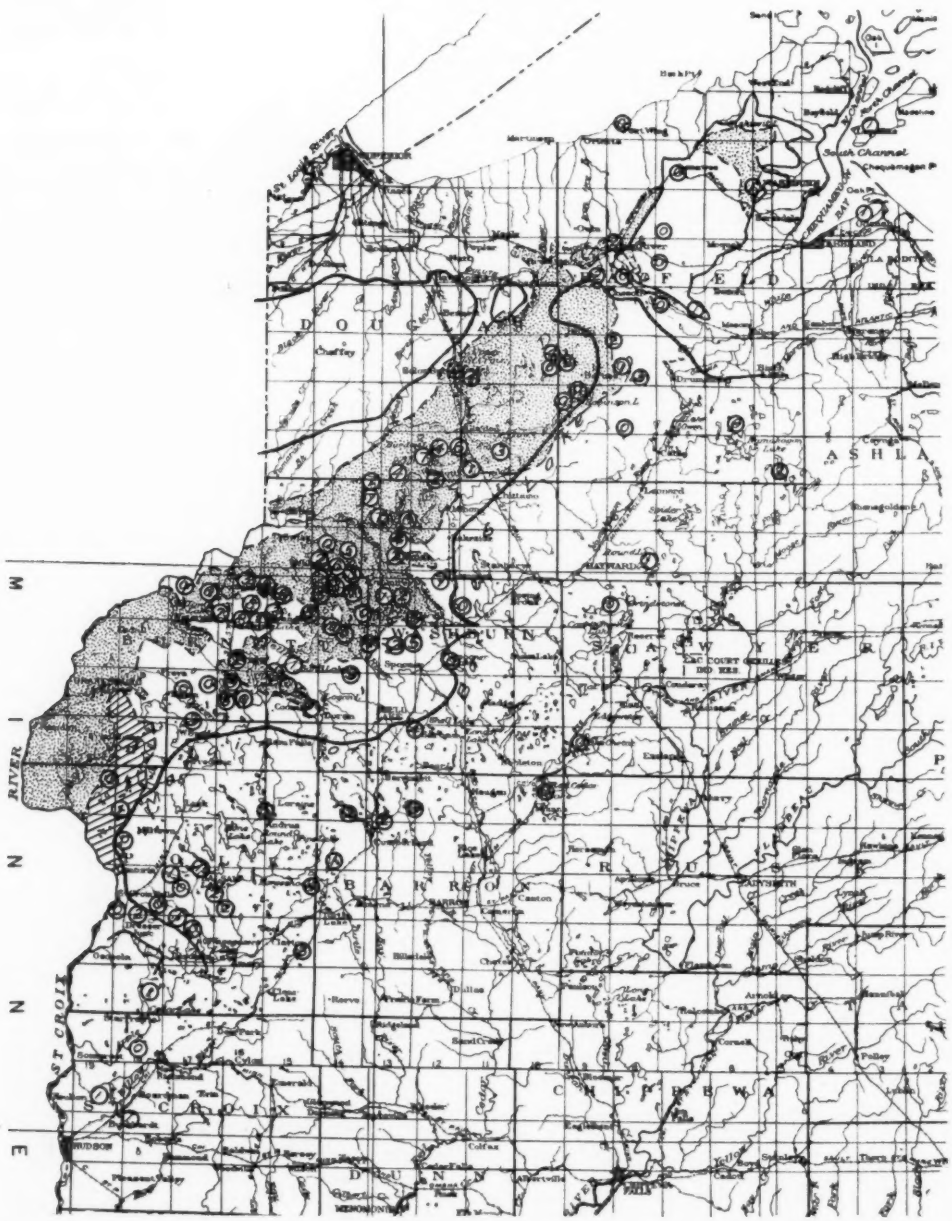


FIG. 29. The distribution of coastal plain plants in northwestern Wisconsin (see list, page 348, in relation to the former pro-glacial Barrens Lake and to the soil factor. The stippled area represents the extent of the light sandy soil; the lined area the calcareous clay of the Grantsburg Moraine. The numbers indicate the numbers of plants from the list which are present on the various lakes.

species from the list. Oak Lake near Gaslyn, Burnett County (Sec. 20, T. 40 no., R. 14 w.) leads with ten. There appear to be several discrepancies in the comparatively large number of species present upon the shores of a few lakes outside the approximate limits of Barrens Lake. Stone Lake near Stone Lake

in eastern Washburn County, Bass Lake near Dueholm, Polk County, and Big Horseshoe Lake north of Turtle Lake, Barron County each has several species from the list. However, an investigation of the species involved discloses the fact that there are comparatively few different ones. These usually include *Bidens connata* var. *pinnata, Juncus pelocarpus, Hemicarpha micrantha,* and *Panicum albemarlense.* It is apparent that there seems to be a tendency upon the part of these species to spread somewhat beyond the limits of the former lake. Many others, not included in the list, also evince this tendency. It may be, therefore, that some of these species, either because of more effective means of seed dispersal (which is not for the most part evident) or because of a lesser degree of ecological specificity, have spread somewhat in more recent times.

An extreme case of this tendency is that of *Polygonella articulata,* which appears to have a coastal plain range with a limited inland extension about the Great Lakes, but which in northwestern Wisconsin has become decidedly weedy in habit, and may be expected wherever there is dry sand. It is not unusual to find it abundant on recent road cuts. Another possible explanation of the occurrence of several of these plants outside of the ancient lake limits is that while the elevation of the lake, as indicated by beaches and littoral features, was never above the 1135 foot contour for any great length of time, the lake may, nevertheless, have stood at a higher level for a brief time, though not long enough to leave clear-cut geological evidence.

It appears rather extraordinary that there should be so much variation in the number of species found upon the lakes within the old lake bed. However, it must be recognized that the lake as a factor in plant distribution was not the only one involved. The soil conditions are of equal importance. It is commonly the case that two lakes, separated from one another by no more than a few hundred yards, may present entirely different topographic and floristic aspects. Particularly striking is the absence of the coastal plain species from southwestern Burnett County. Again the answer is that soil conditions are very different within this part of the county.

The particular significance of the pro-glacial lake as an actual agent in the dispersal of the plants, and as a means of supplying a continuous line of migration suitable to the plants is brought out by the remarkable absence of the coastal plain species from the shores of lakes which were outside the pro-glacial lake basin but which present lithological conditions identical with those of the sandy lakes which lie within the ancient lake limits. Long Lake, nine miles west of the town of Washburn, Bayfield County, lies in an extension of the light sand area of parts of Burnett, Washburn, and Douglas Counties, has a broad sand beach, soft water (pH 6.6), and yet has only the more widely spread forms such as *Dulichium arundinaceum, Scirpus atrocinctus, Solidago graminifolia* var. *Nuttallii, Glyceria canadensis, Agrostis hyemalis, Calama-*

grostis canadensis, Hypericum majus, Agalinis paupercula var. *borealis, Juncus pelocarpus, J. brevicaudatus, Lycopus uniflorus, Lysimachia terrestris, Carex Crawfordii,* and *Juncus effusus.* The explanation lies in the fact that the lake lay at too high an elevation to have been included within the area of Barrens Lake.

Dispersal of the Coastal Plain Plants

The absence of the more conservative coastal plain species from Long Lake where ecological conditions are apparently favorable, but which lay outside of the limits of the ancient Barrens Lake, seems to indicate that these species were following the lake margin very closely. On many other lakes outside the limits of Barrens Lake the sandy shores are duplicated but the coastal plain species are largely absent. What may have been the actual agency of dispersal? A few of these plants, as *Juncus balticus* var. *littoralis,* are propagated by underground stems, but it certainly requires too great a tax on the imagination, even when dealing in terms of geological time, to conceive of this rush as having migrated by means of vegetative propagation, westward about the Great Lakes and into the sand barrens of northwestern Wisconsin. Moreover, most of the species have no such means of spreading.

It is noteworthy that, as Harper ('05) points out, many of these plants with a more limited inland range stand rather low in the scale of vascular plants. Many of them have seeds which are neither attractive to birds or animals, nor adapted to dispersal by wind. There are exceptions, of course, as in the genus Scirpus with its bristles of greater or less length and abundance. In the case of Eriocaulon we find that at maturity the chaffy floral bract and fertile flower float in the breeze, buoyed up by the tufts of hair (Hitchcock and Standley '19, page 115). Despite this fact, however, *Eriocaulon septangulare* is certainly not common everywhere. The genus Bidens, popularly supposed to be dispersed by the lodging of the achene in the hair of the passing animal or in the clothing of some passer-by, varies greatly among its species relative to the frequency of its occurrence. On the sloping sand shores of the northern lakes there is, in many instances, a conspicuous line of chips, driftwood, and debris left each year at the high water level. The occurrence, along this line, of many species of annual plants (Fig. 21) strongly suggests that the seeds of these species are in fact dispersed by the water. The evidence suggests that the spread of at least a considerable number of the coastal plain species was by water currents. In this regard it may seem difficult to conceive of these plants as migrating *up* the outlets of the glacial lakes. Further consideration of this point, however, will recall the fact that in all streams and rivers there are marginal eddy currents which may carry drift for considerable distances upstream. Moreover, the flat, sandy bottoms of the river valleys which once carried glacial streams, such as the

Wisconsin and Mississippi Rivers in Wisconsin, would have been favorable to the development of shifting beds, sloughs, and marginal lakes.

While many of the coastal plain species were limited to the lake and river margins, others were undoubtedly spread, at least to a certain extent, by winds. Moreover, within the sand barrens, and in the adjacent areas, plants of this nature have spread to a greater or less extent in more recent times, and are not strictly confined to the area included within the bed of the ancient lake.

It is at once apparent, however, that some of the more widespread species as *Scirpus americanus* have seeds which are no better adapted to dissemination than other closely related forms as *Scirpus Smithii* which is of far rarer occurrence and of more limited range. The influence of Barrens Lake upon the distribution of the species under consideration was, therefore, in all probability of local and limited importance only. It is evident that there is another, the ecological factor, involved as well.

ECOLOGICAL AND SUCCESSIONAL RELATIONSHIPS WITHIN THE SAND BARRENS

The Soil Factor

Over the greater part of the area included within the bed of Barrens Lake the soil is a light sand. The majority of the lakes are inclosed by gently sloping sandy shores with bars, lagoons, and, in many instances, higher abandoned beaches. These lakes may or may not have outlets, and vary over a considerable range of hydrogen-ion concentration. Numerous tests of the waters indicate that the lakes without inlet or outlet are usually the more acid, while those with inlet and outlet, in many instances kettle depressions in which the streams of the region have enlarged to form lakes, are somewhat more alkaline (Fig. 30). Oak Lake near Gaslyn, Burnett County, has no inlet or outlet. The water showed a pH of 6.4 on August 16, 1929. The sample was taken at the surface, five feet from the shore. When tested a year later, September 10, 1930, the lake water showed the same reaction. On the other hand Web Lake, near the town of Web Lake, Burnett County, is on the Namekagon River, and showed a pH of 8.0. Yellow Lake, near Webster, Burnett County, which is an enlargement of the Yellow River, likewise tests 8.0. The outlet of Big McKenzie Lake, Burnett County, tested pH 7.8, although flowing in an artificial ditch cut through a dry sphagnum bog. The Eau Claire Lakes in southwestern Bayfield County have an inlet and outlet, and again the water is moderately alkaline (pH 8.4). While the lakes within the area of light sandy soil (Fig. 29) generally have a fairly low hydrogen-ion concentration, those which have an inlet and outlet are somewhat "harder" than those in the closed depressions.

There appear to be some striking inconsistencies. Lake Ruth, near Iron

River, Bayfield County, has broad sand shores but a very high pH (9.8). However, this lake lies in an area of stony sand which is the land-deposited moraine of the Superior ice lobe as mapped by Leverett ('29). The alkalinity may, therefore, be due to the presence of calcareous morainic soil which was not reworked and washed by lake action as was the case with the moraines within the Barrens Lake Bed.

Within certain limits there is a decided and immediately noticeable difference in the floras of the "hard" and "soft" water lakes. It is on the sandy shores of the more acid lakes such as Oak Lake that the greatest number of species of coastal plain affinity are found. Among these might be listed *Pontederia cordata, Xyris torta, Eriocaulon septangulare, Juncus pelocarpus, Fimbristylis autumnalis, Lycopodium inundatum, Mariscus mariscoides, Utricularia cornuta, U. gibba,* and *Elatine minima.* In addition there are others of more general range but with a decided preference for the moist, siliceous, sandy shores. Among these are *Cyperus rivularis, Agalinis paupercula* var. *borealis, Panicum huachucae, Lycopus uniflorus, L. americanus, Eupatorium perfoliatum, Echinochloa muricata* var. *microstachya, Carex scoparia, C. Crawfordii, Calamagrostis canadensis,* and *Scirpus americanus.*

On the sandy shores of the alkaline Lake Ruth, however, a quite different line of plants is present. These include *Panicum albemarlense, Cyperus strigosus, Muhlenbergia foliosa, Anemone riparia, Agalinis paupercula* var. *borealis, Lycopus americanus, Astragalus canadensis, Desmodium canadense, Roripa hispida* var. *glabrata, Carex Crawfordii,* and *Stachys palustris.*

In the southwestern part of the area formerly occupied by Barrens Lake in Wisconsin the present lakes appear quite different from those further north. The margins are abrupt, and generally there are extensive stands of *Typha latifolia* adjacent to the shore. The sand margins of the more northern lakes are here replaced by gray clay. Moreover, the lake waters are very alkaline (9.6±). The coastal plain flora is entirely absent from these lakes. The explanation lies in the fact that the late advance of the Wisconsin ice which dammed the glacial water to form Barrens Lake deposited a gray, calcareous clay moraine (Fig. 29). It is in the kettles within this moraine that the lake basins have been formed.

While it is upon the sandy beaches of the "soft" water lakes that the greatest number of coastal plain plants are found, it is, nevertheless, true that a few species of coastal plain affinity prefer the more alkaline lakes. *Echinochloa Walteri* of the eastern fresh and salt marsh borders is found in Wisconsin on the margins of such "hard" water lakes as Lake Puckaway, Green Lake County, in the Fox River Valley. Its only known station in northwestern Wisconsin (in this instance f. *laevigata Wiegand*) is at Yellow Lake, Burnett County, which is a sandy-shored but "hard" water lake. Again *Zizania aquatica* var. *angustifolia,* the northern variety in Wisconsin, appears to occur

only in lakes whose waters exceed pH 8.0. Likewise the common cattail, *Typha latifolia*, does occur on the more acid sandy shores but seems invariably to attain its best development in more alkaline situations.

Zonal Distribution of Plants on the Sand Shores

In September, 1929, a detailed study of the zonal distribution of littoral plants at Devils Lake near Webster, Burnett County (Sec. 3, T. 39 no., R. 16 w.), was made. The lake lies within the area of light sandy soil and within the former bed of Barrens Lake. The present basin was formed as a kettle-hole in the sandy outwash, and was later drowned by the waters of the pro-glacial lake. The total area of the lake at present approximates one square mile. On the southeastern side, where the survey was made, the beach slopes with an extraordinarily gentle pitch, so that the water deepens no more

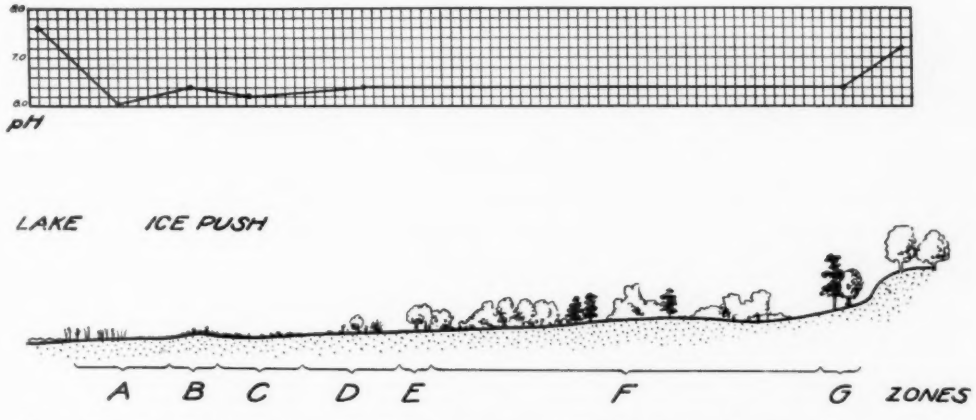


FIG. 30. Zonal distribution of littoral plants at Devils Lake, Burnett County, Wisconsin, in relation to the topography and to the hydrogen-ion concentration.

than three feet 100 feet out from the shore. Back from the water margin a gentle gradient is maintained for approximately 325 feet to the point where there occurs an abrupt rise to the upland surface. Elsewhere, however, the rise is continued more uniformly. About 40 feet inland from the lake margin is a bar which parallels the lake. It was formed in part, probably, by ice push. Behind the bar is a moist, but ordinarily not wet, lagoon. The bar and lagoon are repeated at a point about 225 feet back from the lake margin. This higher bar and lagoon undoubtedly indicate a former higher water level.

Zone A (Fig. 30) extends 40 feet from the water's edge. It is flooded much of the year and during seasons of high water. The sand is saturated, and at all times the water table is close to the surface. Within the strip surveyed there occurs in this zone *Typha latifolia, Sagittaria graminea, S. latifolia* f. *gracilis, Najas flexilis, Scirpus acutus,* and *Juncus pelocarpus.* Nearby, but outside the strip surveyed, *Scirpus americanus* grows in abundance.

Zone B, 14 feet wide, is represented by the somewhat higher and drier surface of the bar. Here, among drift cast up by the lake, is a group of plants which is rather sharply demarcated from that on either side. Among these plants are *Agalinis paupercula* var. *borealis*, *Bidens connata* var. *pinnata*, *B. cernua*, *B. frondosa*, *Cyperus Engelmanni*, *C. rivularis*, *C. strigosus*, *Lycopus americanus*, *Echinochloa muricata* var. *microstachya*, *E. muricata* var. *occidentalis*, *Carex Bebbii*, *C. scoparia*, *Polygonum lapathifolium*, *P. Persicaria*, and *Eupatorium perfoliatum*.

Zone C, 37 feet wide, is again somewhat lower and more moist, but becomes drier toward Zone D. Here are found *Hypericum majus*, *Panicum huachucae*, *Juncus pelocarpus*, *J. brevicaudatus*, *J. balticus* var. *littoralis*, *Fimbristylis autumnalis*, *Spiranthes cernua*, *Pinus resinosa* (three year old seedling), *Betula papyrifera* var. *cordifolia* (seedling), *Ranunculus reptans*, *Lycopodium inundatum*, *Xyris torta*, and *Drosera rotundifolia*.

Zone D, 40 feet wide, is marked by the presence of an abundant two-foot growth of poplar and willow. Here are *Salix Bebbiana*, *S. discolor*, *S. petiolaris*, *S. humilis*, *Hypericum majus*, *Agalinis paupercula* var. *borealis*, *Fragaria virginiana*, *Lycopus americanus*, *Spiraea tomentosa* var. *rosea*, *Populus tremuloides*, *P. balsamifera*, *Solidago graminifolia*, *Polygonella articulata*, *Rhus Toxicodendron*, *Hudsonia tomentosa* var. *intermedia*, *Erigeron ramosus*, *Gnaphalium obtusifolium*, *Aster azureus*, and *Helianthemum Bicknellii*.

Zone E, 12 feet wide, is dominated by six-foot poplars. Here are found *Hypericum majus*, *Agalinis paupercula* var. *borealis*, *Fragaria virginiana*, *Lycopus americanus*, *Spiraea tomentosa* var. *rosea*, *Populus tremuloides*, *P. balsamifera*, *Agrostis alba*, *Erigeron ramosus*, *Solidago graminifolia*, *Aster azureus*, *Gnaphalium obtusifolium*, and *Helianthemum Bicknellii*.

Zone F, 160 feet wide, is dominated by larger trees. These tend to be grouped in clumps, leaving open, dry, sandy areas interspersed. Among the species occurring in this zone are *Pinus resinosa*, *P. Banksiana*, *Populus tremuloides*, *P. balsamifera*, *Rhus typhina*, *Fraxinus pennsylvanica* var. *lanceolata*, *Betula papyrifera* var. *cordifolia*, *Salix humilis*, *Agrostis alba*, *Calamagrostis canadensis*, *Panicum huachucae*, *Prunus pennsylvanica*, *Spiraea tomentosa* var. *rosea*, *Juncus balticus* var. *littoralis*, *Hieracium canadense*, and *Solidago graminifolia*.

Zone G, 15 feet wide, is a transitional zone between the sand beach and the mixed woods. It includes the abruptly rising banks. Here are Pinus resinosa (large tree), *Betula papyrifera* var. *cordifolia*, *Quercus rubra*, *Vaccinium pennsylvanicum*, and *Anaphalis margaritacea*.

As a result of hydrogen-ion determinations made within the different zones a striking correlation with moisture content of the sand was obtained (Fig. 30). The method for making these determinations was to dig a series

of test wells eight inches deep in which seepage water was allowed to collect. Determinations were made by the colorimetric method. It was found that whereas the lake water three feet out from the shore at the surface tested pH 7.6, the seepage water 20 feet inland from the lake margin tested pH 6.0. This remarkable drop suggested that the increasing acidity might be due to seepage through the siliceous sands. The lake water immediately adjacent to the sandy margin was next tested. The result, pH 7.2, was somewhat lower than in the case of the water taken three feet out. This fact strongly suggested that the increasing acidity of the seepage water was due to some factor of a lithological nature.

Further tests gave interesting results. On the drier ice push the pH was found to be 6.4, whereas in the more moist lagoon it again dropped to 6.2. With increasing elevation back from the lake margin there was a return to 6.4, and this figure remained constant until in the upland woods the pH was found to be 7.2. In considering these facts it is interesting to note the remarks of Kearney ('04) relative to the soluble salts of sandy coastal beaches and their possible relationship to the littoral flora. "All the beach and dune soils examined along the Atlantic coast of the United States contained a considerable amount of water at a slight depth below the surface, which is, indeed, a well-known peculiarity of such soils. The data given make it evident that the water does not come from the sea unless we assume that sea water, moving through but a few meters of sand, will give up nearly all the soluble salts it normally contains."

It would seem that this assumption may, in fact, be well founded. Tests of hydrogen-ion concentration within the sand barrens have confirmed for this region the work of Wherry ('23), Salisbury ('22), and other workers in finding that on the uplands the leaching tends to reduce the carbonate content of the upper soil layers, and to concentrate the salts at a lower level. This would be true only where precipitation is sufficient to offset the effect of evaporation, with the marked upward movement of the ground water and its contained salts. The "alkalie flats" of the arid regions of the west are the result of such conditions. It appears entirely probable that the sandy lake shores, exposed to the full heat of the sun and supplied from below with water, are losing an excess of moisture by evaporation. It seems likely that this tendency would result in the concentration of the salts at a point above the level of the water table. This would tend to deprive the sand below the water table of its carbonate content, and as a result the water from these lower sands would have a considerably lower hydrogen-ion concentration. This hypothesis seems entirely in agreement with the results obtained at Devils Lake.

There is another factor which may influence, to a certain extent, the hydrogen-ion concentration of the ground water in the sands. Mr. C. Juday

has informed me that the waters of many of the sandy-shored lakes show traces of silicates. It seems entirely possible that the increased moisture may bring about a greater degree of solution of the soluble silicates and thus lower the pH. These conclusions are opposed to those of Jewell and Brown ('29) who found similar stratigraphic differences on the lakes of northern Michigan and explain the acidity of the seepage water as due to organic acids produced in the lake margin and carried into the lake. In many instances there appears to be little doubt but that marginal vegetation and the partial decomposition of organic material does result in increased acidity. However, in the tests at Devils Lake particular care was given to the possibility of there being organic material present in the test wells or in the adjacent sands, and in no case was any found in sufficient quantity to explain the results.

Plant Succession within the Bed of Barrens Lake

In addition to the lakes of various character there are, within the sand barrens of northwestern Wisconsin, many square miles of acid bog or "muskeg." These bogs may be found in all degrees of development upon the lakes, and, in many instances, are found to be forming within a bay off the open lake. At Johnson Lake, near Oakland, Burnett County, the bog is developing within a long narrow portion of the lake which has been cut off from the lake proper by a sand bar. (Fig. 22). The bogs support, in the more moist sphagnum, such typical acid bog species as *Andromeda glaucophylla, Chamaedaphne calyculata, Vaccinium macrocarpon, Sarracenia purpurea, Hypericum boreale, Lycopodium inundatum, Hypericum virginicum, Dorsera rotundifolia,* and *Eriophorum virginicum* f. *album.* Near the margins, and adjacent to an "island" which supports a stand of mature trees of *Pinus Strobus* the bog has become drier (Fig. 23), and the heaths are replaced largely by *Spiraea tomentosa* var. *rosea, Scirpus cyperinus* var. *pelius, Polygonum punctatum* var. *leptostachyum, Hypericum virginicum, Carex scoparia, Agrostis hyemalis,* and *Leersia oryzoides,* with *Pinus Banksiana, P. Strobus, Picea canadensis, Populus balsamifera,* and *P. tremuloides* invading from the margin.

Elsewhere this dry bog stage has become dominant, and the heaths are entirely absent or only occasional over the entire bog surface. Under such conditions the surviving coastal plain types are limited to those which show a preference for the marginal dry, sandy, abandoned shore lines, and include *Panicum meridionale, P. albemarlense,* and *Juncus balticus* var. *littoralis.*

In parts of the sand barrens, particularly in Douglas and Bayfield Counties, where, within the past forty years, lumbering and extensive fires have been the rule, there is no longer any evidence of the wet bog associations. The depressions have become quite dry, and are being occupied by species of oak, popular, and birch together with *Prunus pennsylvanica, Pinus Banksiana,* and with an undergrowth including *Vaccinium pennsylvanicum,*

Pteridium latiusculum, *Arctostaphylos uva-ursi* var. *coactilis*, and *Myrica aspenifolia*. There are also a number of representatives of the invading prairie flora.

There thus appears to be a definite successional sequence on the acid sandy-shored lakes which may be summed up as follows: 1. Sandy-shored lake with the coastal plain flora generally well represented. 2. Development of sphagnum bog with characteristic heath flora, and the crowding out of the great part of the sandy shore flora. 3. With increasing dryness, the replacement of the sphagnum bog by a "bog meadow" association. 4. Final occupancy of the abandoned shores by the dry barrens and prairie flora or by a mixed woodland where heavier soil favors the development of such an association.

Another successional phase appears to develop where, as at Johnson Lake (Fig. 24), the margin of the lake proper is occupied by swales with an extensive development of *Typha latifolia*, *Phragmites communis*, *Pontederia cordata*, *Dulichium arundinaceum*, *Sagittaria latifolia*, *Eriocaulon septangulare*, *Juncus effusus*, *Scirpus Torreyi*, *S. americanus*, *S. validus*, *Carex comosa*, and *Castalia odorata*. In the more alkaline lakes *Zizania aquatica* var. *angustifolia* is apt to be very prominent. Apparently, however, the swale margins represent an intermediate phase which would be replaced by sphagnum bog unless there is an inlet and outlet to the lake when this phase seems to assume a greater degree of permanence due to the maintainance of the water level.

THE COASTAL PLAIN FLORA AS A RELIC FLORA

Endemism

To a certain extent the use of the term "relic" as applied to a group of plants manifesting a certain similarity of distribution in response to environmental and distributional factors is a relative matter. Endemism, due to isolation over a long period of time, is generally considered a criterion of such a relic flora. Fernald ('25, page 294) contrasts the western and endemic species centering on the Gulf of St. Lawrence, a flora including some 80 endemic species, with the flora of coastal plain derivation now isolated in Nova Scotia as a result of the submergence of the northern continental shelf. He writes, "These are all plants derived from the southern coastal plain, some of them unknown nearer than the Carolinas, and nearly all characteristic of the sandy coastal strip from southern New Jersey to Florida and Mississippi, there occurring in a climate obviously much warmer than that of the foggy coast from Digby and Yarmouth Counties to Guysborough, Nova Scotia. Yet in the 25,000 years (more or less) since the flora of far-southern origin became isolated on the Atlantic slope of Nova Scotia it has set off only a single endemic species, and that a rapidly reproducing annual, the specific validity of which has been doubted. Otherwise the most Nature has accom-

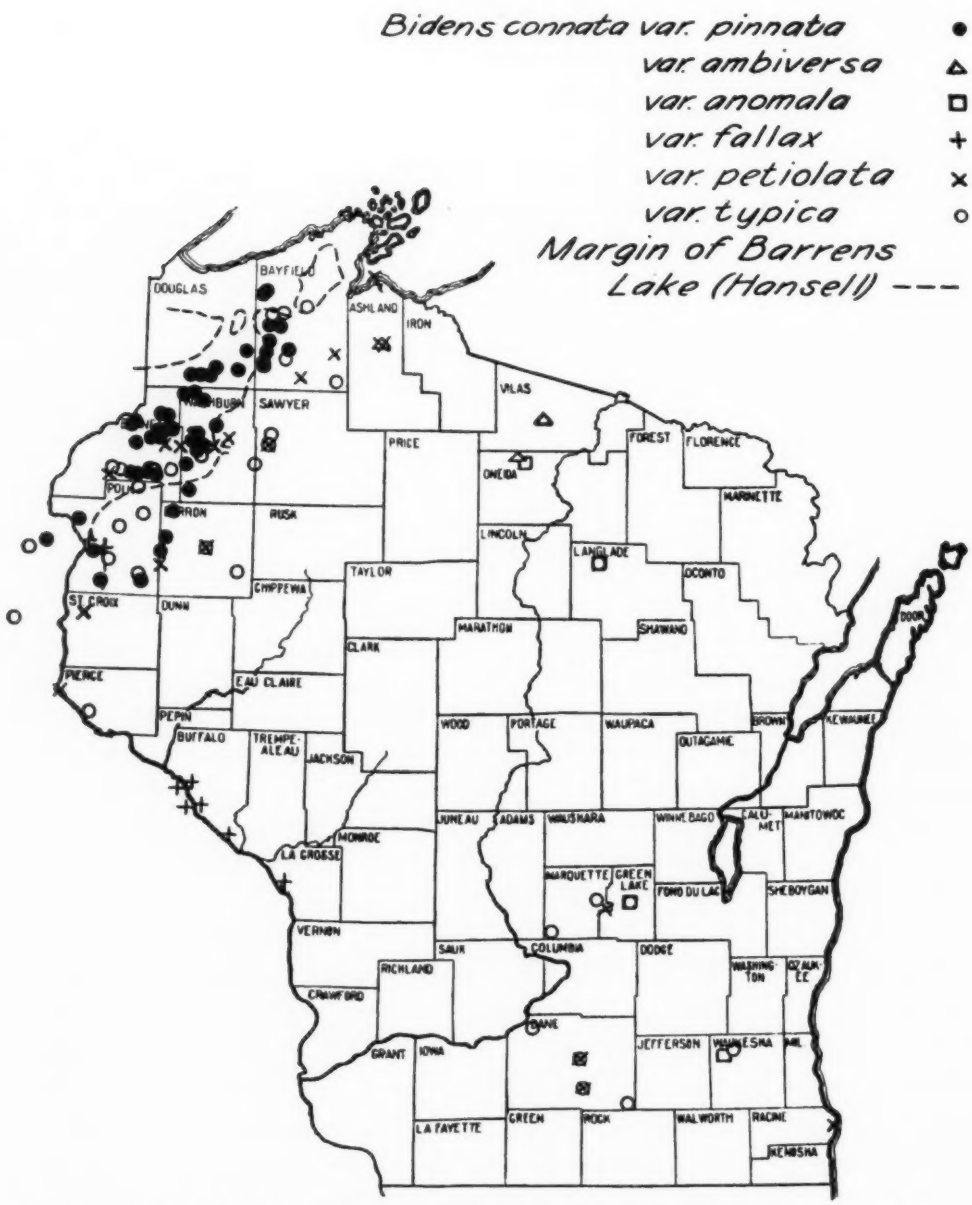


FIG. 31. The distribution of *Bidens connata* and varieties in Wisconsin. Var. *pinnata* is endemic to the northwestern sandbarrens.

plished in Nova Scotia toward segregation from the southern types is the slight increase of hairiness or the modification of structure or foliage in about a dozen species."

It is interesting to compare this situation in Nova Scotia with that in the sand barrens of northwestern Wisconsin. The only endemic to the region formerly occupied by Barrens Lake and to the immediately contiguous areas is *Bidens connata* var. *pinnata*, originally described from Hennepin County,

Minnesota, an area now considered to have been covered by a glacial lake which may have been an extension of Barrens Lake (Hansell '30).

Moreover, the *Bidens connata* group, well-known for its variability, includes a great complexity of forms with rather definite and significantly localized ranges within Wisconsin (Fig. 31). Of the six recognized varieties (Fassett '28) one, var. *pinnata*, is practically limited to the Barrens Lake area; a second, var. *fallax*, occurs in the Mississippi bottoms and in the southern and more calcareous part of the Barrens Lake bed, and var. *ambiversa* is known from the sphagnum bogs adjacent to the northern lakes. The others, vars. *petiolata*, *typica*, and *anomala* are more generally distributed.

In view of the history of the plant migrations these three more localized forms are of particular interest, and suggest variation due to changing ecological conditions and partial isolation, in the Mississippi bottoms, in the northern bogs, and within the Barrens Lake region. The divergent effect of the lithological differences is further suggested by the fact that var. *pinnata* attains its extreme of leaf division within the more circumscribed area of light acid sands, and elsewhere is, in many cases, intermediate with the more generalized types (*typica* and *petiolata*).

While the variable *Bidens connata* group alone has succeeded in developing a true endemic variety, the influence of the soil factor may be observed elsewhere in the reduction of leaf size, and in the general dwarfing of a number of other species among which *Hypericum majus* and *Typha latifolia*, on the sand shores, stand out conspicuously.

It is apparent, then, that while the coastal plain flora within the sand barrens is a conservative rather than an aggressive element, one that seems destined within a comparatively short time to extinction within the region, it is, nevertheless, a youthful flora as judged by the standard of endemism.

Possibility of Persistence in Driftless or Unglaciated Areas

It is entirely within the realm of possibility, insofar as the present knowledge of Pleistocene geology extends, that the conditions favorable to the inland extension of the coastal plain element which were an accompaniment and result of the last or Wisconsin glaciation, may have been duplicated by previous stages of ice advance. It is, therefore, possible that the coastal plain flora had extended inland at least once previous to the Wisconsin stage, and would have then been eradicated in the regions covered by later ice. The question arises, therefore, as to whether these plants may not have persisted within The Driftless Area of southwestern Wisconsin, and later have migrated northward upon the final retreat of the ice, to establish themselves within the sand barrens.

Recently discovered deposits of plant remains in the vicinity of Baraboo, Sauk County, Wisconsin, near the eastern border of The Driftless Area, are

tentatively dated by Mr. F. T. Thwaites of the Geology Department of the University of Wisconsin as of pre-Wisconsin age.

Again there is some evidence from the distribution of a few species including *Hypericum Kalmianum*, a species endemic to the Great Lakes region, occurring in The Driftless Area, and not extending elsewhere beyond the limits of glaciation (McLaughlin '31), that some forms may have remained as relics within The Driftless Area, and have later extended eastward.

There is little evidence from the range of the coastal plain species, however, to warrant the supposition that they may have had a similar history. If they had taken refuge in the unglaciated region, and later migrated northward and westward we should be justified in expecting that there would be a much larger number of species still remaining; more, in fact, than in other nearby regions as the Indiana Dunes, but this is not the case.

The present occurrence of coastal plain plants within The Driftless Area is related to two facts. The greater number, occurring within the Wisconsin River bottoms as at Arena, Iowa County, quite obviously owe their presence there to factors directly related to the Wisconsin stage of glaciation. Those species which are more widespread in The Driftless Area, for example *Polygonella articulata* and *Vaccinium macrocarpon*, are species which are of fairly general distribution throughout the state wherever conditions favorable for their growth are found. The weedy nature of the *Polygonella* has already been suggested. It is reasonably evident that this Driftless Area occurrence is a more recent phase in the migration of these species, and cannot be taken to indicate a relic relationship.

The Possibility of Persistence at the Southern Extent of Glaciation

Similarly the possibility of persistence in favorable areas beyond the southern extent of glaciation does not seem tenable. The Nebraska Sand Hills region, lying but a short distance beyond the margin of Wisconsin glaciation, harbors but 13 of the 90 species and varieties listed by Peattie, and these are types which are of more general occurrence westward such as *Aristida tuberculosa, Hemicarpha micrantha, Juncus balticus* var. *littoralis*, and *Nelumbo lutea*. The old idea of plants migrating southward before the advancing ice, and later returning northward, failed to take into consideration the problems of dispersal, and the high degree of specificity of many species regarding their climatic and lithological requirements.

CONCLUSIONS

1. The occurrence of a considerable number of species of Atlantic Coastal Plain affinity within the sand barrens of northwestern Wisconsin appears to be dependent upon two factors: (a) the presence of favorable soil and climatic conditions within the region, and (b) the former greater extent of

these requisite conditions so that a more or less continuous pathway for the inland migration of these coastal plain types from the coastal plain proper was existent.

2. The greater number of coastal plain plants within the region are highly specific in their soil requirements, and grow upon the moist sandy shores of some of the lakes within the region. Other coastal plain types are found associated with swales and marshy margins of the lakes, conditions simulating those under which they grow upon the coastal plain.

3. The region within the sand barrens which harbors the greater number of these plants lies within the bed of a pro-glacial and early post-glacial lake which has been recently recognized upon geological evidence. The present lakes, on the margins of which and in the waters of which the plants grow, indicate by their higher abandoned beaches that they are relics of larger bodies of water. The occurrence of the plants upon the lake shores suggests that they occurred upon the margin of the larger body or bodies of water, and have become isolated upon the present lakes as the water level dropped. The absence of the plants from the shores of other lakes whereon the ecological conditions are favorable but which were outside the probable limits of the pro-glacial "Barrens Lake" further supports the suggested relationship between the migration of the plants and the pro-glacial lake. The comparative absence of the plants from lakes with clay margins or with highly calcareous waters, but within the former extent of the ancient lake, is due to the absence of soil conditions favorable for their growth.

4. The coastal plain types within the region are at present gradually losing ground before the advance of the more aggressive floras such as that of the prairies, on the one hand, and of the sphagnum bog, on the other. Due to artificial draining, extensive lumbering, and burning of the original forest cover, many of the lakes have, in recent time, become dry, and the habitat unfavorable for the coastal plain species.

5. While the coastal plain species are not strictly limited to the region within the bed of the "Barrens Lake," those species which are most commonly found outside this circumscribed region are those which are more general in distribution elsewhere, and appear to be less specific in their ecological requirements or to have more effective means of seed dispersal. The absence of the more conservative species from nearby regions with favorable ecological conditions, but which were probably outside the limits of the "Barrens Lake" disfavors the possibility of seed dispersal in comparatively recent times by birds, winds, or other chance agencies.

6. The failure of certain species with a northern and coastal range to extend into the sand barrens suggests that these plants extended into the region at a time (probably later than that of the coastal plain flora) when there was no connective suitable for the migration of the plants between the Superior Basin and the "Barrens Lake."

7. The occurrence of many species which are present in the sand barrens of northwestern Wisconsin elsewhere in the state; namely within the Fox River Valley, the bottoms of the Wisconsin River and of the Mississippi River, where conditions resulting from the last glaciation are favorable to the growth of the plants, suggests that these regions formed a pathway for the migration of the coastal plain element westward and northward from the region of Lake Michigan. Another path of migration into the interior of Wisconsin was from the southern coastal plain up the Mississippi River, but species, as *Lophotocarpus calycinus* which show this range have not extended northward into the sand barrens.

8. The present distribution of the coastal plain element inland disfavors the possibility of the persistence of the plants within The Driftless Area of Wisconsin or at the southern extent of the ice during the last glaciation.

9. The time at which the migration occurred is set at early post-glacial, and cannot be determined more specifically at present due to the as yet imperfect knowledge of the glacial history of the region.

10. A single endemic, *Bidens connata* var. *pinnata* is known within the region included in the bed of the ancient lake, but other species on the acid sand shores of the lakes tend to manifest a degree of dwarfing, and a reduction of leaf surface.

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FUMIGATION AND CIGARETTE BEETLES

A CORRECTION

In a paper[1] recently published by the writer there were errors which give wrong impressions of the relative values of fumigants used in experiments with cigarette beetles. These errors have been called to my attention by Mr. William Moore, of the American Cyanamid Sales Company, to whom I extend my grateful acknowledgments. In Tables XXIV and XXV concentrations of fumigants used are stated in pounds per 1000 cu. ft. The figures are in each 4.86 times too low. In other words, when the tables show one pound of fumigant per 1000 cu. ft. there were 4.86 lbs. This error applies to the statements concerning ethylene oxide, ethylene dichloride, carbon tetrachloride, chlorpicrin, carbon disulphide, and carboxide. Not only the tables but Figs. 19 and 20 and the statements under "Experimental Results," which are based on the tables, are thus incorrect. Pounds per cubic feet should be multiplied by 4.86 in each case. The writer's findings in regard to cyanide were in error because of the use of concentrated sulphuric acid and sodium cyanide as a source of hydrocyanic acid instead of a mixture of sulphuric acid, water, and sodium cyanide. When concentrated sulphuric acid acts upon sodium cyanide, gases other than hydrocyanic acid are produced. These gases are combinations of carbon monoxide, carbon dioxide, sulphur dioxide, and ammonia, depending upon the proportions and the conditions of the experiment. The proportions used in the experiments were such as to produce only a small percentage of hydrocyanic acid gas. Hence, the entire section devoted to hydrocyanic acid gas, including the table and figure, is incorrect and has no bearing upon the effectiveness of hydrocyanic acid gas as a fumigant for the cigarette beetle. Some of the experiments will be repeated and extended. It is hoped that more definite conclusion may thus be reached.

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[1] An ecological study of the tobacco beetle, *Lasioderma serricorne* Fabr., with special reference to its life history and control. Ecol. Monogr., 1:333-393, 1931.